

A SYSTEMATIC REVISION OF
THE SABELLIDAE-CAOBANGIIDAE-
SABELLONGIDAE COMPLEX
(ANNELIDA: POLYCHAETA)

KIRK FITZHUGH



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ABSTRACT

A cladistic analysis is conducted, encompassing a series of hierarchical levels within the Sabellidae-Caobangiidae-Sabellongidae complex. Generic relationships within this complex are examined using 36 genera and 43 characters. Outgroup comparisons with the Serpulidae s.s. and Spirorbidae are initially suggested. It is argued, however, that maintaining the Spirorbidae results in the Serpulidae being paraphyletic. Therefore, the Serpulidae s.l. (including spirorbids) are used as the outgroup. The possibility of using the Terebellomorpha (= Terebellida) as an outgroup is discussed. The more inclusive relationship between the orders Sabellida and Spionida is examined, leading to the conclusion that the Spionida is paraphyletic by way of recognizing the Sabellida. Sixteen most parsimonious cladograms are found, differing only slightly in the placement of some genera. *Caobangia* Giard and *Sabellonga* Hartman, representing the monotypic Caobangiidae and Sabellongidae, respectively, fall within the Sabellidae. In order to define the Sabellidae as monophyletic, *Caobangia* and *Sabellonga* must be placed in this family. Present sabellid subfamilies are either paraphyletic or polyphyletic, except for the monotypic Myxicolinae. Revised monophyletic subfamilies are suggested, comprising a more restricted Fa-

briciinae and expanded Sabellinae. *Caobangia* is placed into the former subfamily, while *Sabellonga* is moved to the latter. The Myxicolinae is not recognized, with *Myxicola* Koch in Renier being placed in the Sabellinae. Genera of the revised Sabellidae are reviewed in light of the characters used in the cladistic analysis. Several genera are poorly defined in terms of monophyly (e.g., *Oriopsis* Caullery and Mesnil, *Jasmineira* Langerhans), while six genera are not defined by synapomorphies: *Chone* Kröyer, *Sabellastarte* Kröyer, *Perkinsiana* Knight-Jones, *Pseudopotamilla* Bush, *Eudistylia* Bush, and *Schizobranchia* Bush. Setal transformation series are discussed, suggesting the presence of regulatory mechanisms localized within a particular body region or operating throughout the thorax and abdomen. Such mechanisms appear to allow for considerable structural lability, resulting in convergence of thoracic and abdominal setal forms from different plesiomorphic states. In some cases, it also appears as though abdominal setal forms may be controlled by segment age and location along the body. Changes in thoracic or abdominal setal forms in notopodia and neuropodia within a particular segment appear to be independent of one another.

INTRODUCTION

The polychaete order Sabellida (sensu Fauchald, 1977 and Knight-Jones, 1981, in part; Holthe, 1986) has been considered by some workers to include up to six families: Sabellariidae Johnston, 1865, Sabellidae Johnston, 1846, Caobangiidae Jones, 1974a, Sabellongidae, Hartman, 1969, Serpulidae Johnston, 1865, and Spirorbidae Pillai, 1970. The order can be considered monophyletic on the basis of the phenomenon of setal inversion, in which the abdominal region of the body is denoted by the occurrence of notopodial uncini and neuropodial capillary (or similar) setae. Traditionally, however, placement of these families into a more inclusive hierarchical grouping has varied. Members of this order have usually been allied in varying degrees with families outside the order because of their sedentary, tubicolous nature and general body appearance.

Exclusive of the Sabellariidae and Sabellongidae, members of the Sabellida are quite distinctive in possessing a branchial crown.

The Serpulidae and Spirorbidae appear to form a monophyletic group based, in part, on the formation of a calcareous tube. There appear, however, to be definitional problems with the Sabellidae, Caobangiidae, and Sabellongidae. The Sabellidae are distinguished from the serpulids and spirorbids in possessing thoracic neuropodial uncini in which the distal end is composed of a main fang surmounted by a series of smaller teeth. The Sabellongidae have been reported to have a pair of palplike structures replacing the branchial crown (Hartman, 1969); their thoracic neuropodial uncini are the same as those seen in the Sabellidae. In addition, sabellongids have thoracic neuropodial companion setae similar to those seen in some genera of sabellids. The Caobangiidae are distinctive in having a recurved gut which opens anterodorsally into a dorsal groove and the complete loss of thoracic neurosetae (discussed below). The caobangiids possess a branchial crown which is supported by a "cartilagi-

nous" skeleton which appears, at least initially, to be homologous to that of most sabellids (but see below). As a result, there are no character(s) which can define traditional Sabellidae as a monophyletic group. The Caobangiidae and Sabellongidae are monotypic families containing *Caobangia* Giard and *Sabellonga* Hartman, respectively.

I suggest that the definitional problems of the Sabellidae stem from the fact that the family is paraphyletic as a result of recognition of the Caobangiidae and Sabellongidae. The first objective of this paper is to establish the validity of a general sister-group relationship between the Sabellidae-Caobangiidae-Sabellongidae complex and other families of the Sabellida. For this to be accomplished, a necessary revision of the Serpulidae-Spirorbidae complex is presented. Then, the present concept of the orders Sabellida and Spionida is shown to be less informative in the cladistic sense in that recognition of the Sabellida results in the Spionida being paraphyletic. At this point, a monophyletic outgroup to the Sabellidae-Caobangiidae-Sabellongidae complex can be hypothesized. A second objective is a cladistic analysis of the genera of the Sabellidae, Caobangiidae (*Caobangia*), and Sabellongidae (*Sabellonga*). These results demonstrate a need to include *Caobangia* and *Sabellonga* in the Sabellidae. The adequacy of the present sabellid subfamilies also is evaluated on the basis of this cladistic analysis.

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FIGURE ABBREVIATIONS

b	breast
bay	bayonet setae
bc	anterior peristomial ring collar
bh	branchial heart
bl	branchial lobe
bs	anterior peristomial ring
bv	blood vessel
c	coelom
ce	compound eye
co	posterior peristomial ring collar
comp	companion setae
cs	posterior peristomial ring
ct	connective tissue
dbbf	dorsal branchial base flange
df	dorsal branchial fusion
dl	dorsal lip
dpa	dorsal pinnular appendage

dra	dorsal radiolar appendage	ps	pinnular skeleton
gg	glandular girdle	r	radiole
h	hood	rf	radiolar flange
inf	inferior notosetae	rs	radiolar skeleton
man	manubrium	se	simple eyespot
n	neck	setf	setal fascicle
neuop	neuropodium	spine	spinelike setae
nl	ventral narrow lobe extension of anterior peristomial ring	ss	skeletal sheath
noto	notopodium	st	stylope
nvfa	nonvascularized, ventral filamentous appendage	sup	superior notosetae
pal	palcate setae	unc	uncini
pe	pygidial eye	vbf	ventral basal flange
pi	pinnule	vl	ventral lip
pig	pigment	vra	ventral radiolar appendage
pl	parallel lamellae	vs	ventral sac
pm	palmate membrane	vvfa	vascularized, ventral filamentous appendage
pr	peristomium	wl	ventral wide lobe extension of anterior peristomial ring

DEVELOPMENT OF THE "SABELLIDA" CONCEPT

One of the earliest classifications recognizing general similarities among groups currently placed within the Sabellida was made by Lamarck (1818), in which he separated the annelids into two major groups: errant and tubicolous forms. Within the tubicolous group he further separated genera into two subgroups; those producing soft tubes and those secreting calcareous tubes. Genera producing soft tubes included *Terebella* Linnaeus, *Sabellaria* Lamarck, *Pectinaria* Lamarck, and *Amphitrite* Müller (= *Sabella* Linnaeus, in part); while those producing calcareous tubes included the presently recognized serpulids, *Serpula* Linnaeus and *Galeolaria* Lamarck, and the spirorbid *Spirorbis* Daudin.

Savigny (1822) later established the order Serpuleae, in part comparable to Lamarck's (1818) tubicolous group, and containing three families. Of these, the family Amphitritae consisted of three sections: *Amphitrites sabelliennes* (with *Serpula* and *Sabella*), *Amphitrites hermelliennes* [with *Hermellia* (= *Sabellaria*)] and *Amphitrites terebelliennes* (with *Terebella* and *Amphictene* Lamarck). Burmeister (1837) raised Savigny's section *Amphitrites sabelliennes* to family level, as the family Serpulacei. The group was then split into two families, Sabellidae and Serpulidae, by Johnston (1846). Grube (1850)

accepted Burmeister's family, although he spelled it Serpulacea, and established the family Hermellacea (= Sabellariidae) for Savigny's *Amphitrites hermelliennes*. Grube denoted the general grouping of these families with other sedentariate families.

In his work on the Arctic polychaetes, Malmgren (1866) split the family Serpulacea into three families: Sabellacea (now Sabellidae), Serpulacea (Serpulidae), and Eriographidea (or Eriographidae, with *Myxicola* Koch in Renier). He did not consider the sabellariids, which were not present in his material. Claparède (1868) maintained the family Serpulacea (sensu Grube, 1850), dividing the sabellids and serpulids into the tribes Sabellides (including *Myxicola*) and Serpulides, respectively. The two tribes had roughly the content of the modern families by the same names. He also recognized the family Hermelliens but did not comment on any affinities between the serpulaceans and hermelliens. In his comments on Malmgren's (1866) three families, Claparède (1868) stated that he considered the Serpulacea to be "perfectly natural." It is not clear what Claparède meant by the term "natural" in this context. Claparède's (1868) system was adhered to in large part by Saint-Joseph (1894). Later, Claparède (1870) removed *Myxicola* from the Sabellides, placing it into a new tribe,

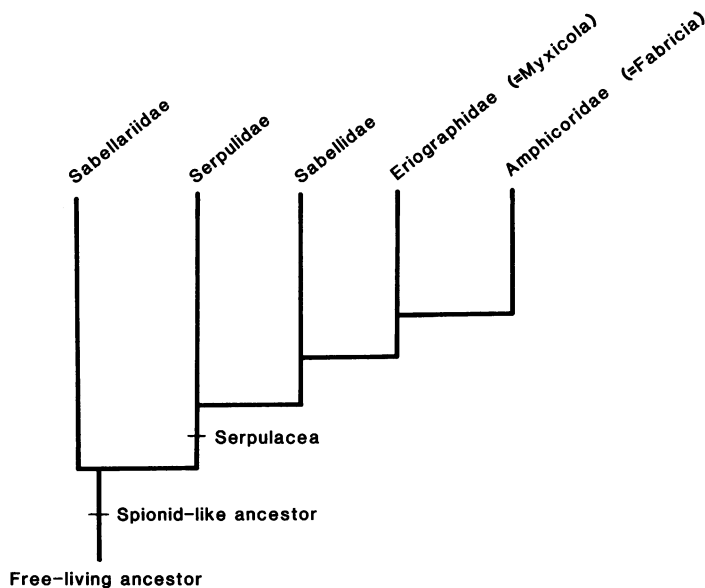


Fig. 1. Diagram (slightly modified) used by Meyer (1888) to denote phylogenetic relationships of the Sabellariidae and "Serpulacea."

Eriographides, thus effectively copying Malmgren's system at a slightly different hierarchical level.

In his notable study on the morphology/structure of the anterior region of the sabellariids, sabellids, and serpulids, Meyer (1888) appeared to base his system on the classifications of Grube (1850) and Malmgren (1866). In the "Serpulacea," Meyer recognized what I interpret to be four families: Serpulidae, Sabellidae, Eriographidae, and Amphicorinidae (including *Fabricia* Blainville). No formal description was given for the Amphicorinidae and I consider this to be actually nothing more than an informal grouping by Meyer. While Meyer made no major changes in the composition of the families, except in recognizing the Amphicorinidae, his views on phylogenetic relationship have had an important impact. In a discussion on relationships, Meyer illustrated a branching diagram which closely resembles the logical pattern of modern cladogram construction (fig. 1), in which ancestral forms with shared derived characters were hypothesized and indicated on the figure to some extent. Recognition of a sister-group relationship between the sabellariids (Hermellidae) and serpulaceans was based in part on the common possession of tentacular feeding

structures surrounding the mouth, a common opening for thoracic nephridia, retraction of the head region into the thorax, presence of ventral shields, and setal inversion. Meyer suggested that these shared characters would have been possessed by the common ancestor of both groups. The sabellariids were considered primitive relative to the serpulaceans, with both taxa being derived from a spioniiform ancestor. According to Meyer, the more primitive nature of the sabellariids was indicated in part by the common possession of distinct palps, the presence of notosetae and neurosetae on setiger 1 and the occurrence of dorsal parapodial gills and ventral cirri on the thorax and abdomen—all features present among various spioniiforms.

Among the Serpulacea, the serpulids were considered to be the most primitive group primarily on the basis of the thoracic membrane supposedly being homologous to fused dorsal gills and ventral cirri. This also implied, by necessity, that the thoracic membrane had been secondarily lost in the sabellids. The simple construction of the dorsal and ventral lips and lack of a palmate membrane in the serpulids were additional characters denoting this relationship. Meyer speculated that the serpulacean ancestor inhabited hard substrates, where availability of sedi-

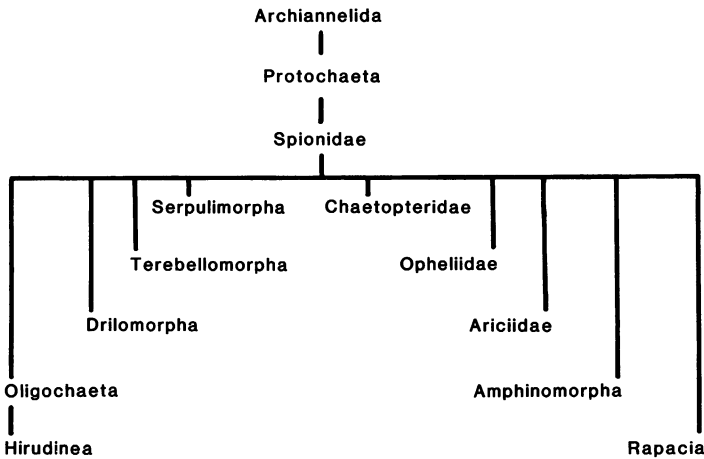


Fig. 2. Phylogenetic tree (slightly modified) presented as figure 1 in Hatschek (1893).

mentary particles for tube construction would have been minimal. Therefore, selective pressures resulted in the production of calcium carbonate tubes by the serpulids and horny, mucoid tubes by the sabellids. At some later time, sabellids began to inhabit soft substrates, resulting in the investment of sediment into tube construction. Meyer's views on relationships between the sabellids, eriographids, and amphicorinids are discussed below in the section on sabellid subfamilies.

Orrhage (1980) stated that Meyer's main arguments for a sister-group relationship between the sabellariids and sabellids-serpulids were based on the assumed homology of the anterior tentacular structures and the presence of a common pore for thoracic nephridia. Orrhage confirmed the latter observation but pointed out that the tentacular structures are not homologous (see also Orrhage, 1978). Orrhage (1980) did not, however, mention that setal inversion is still a synapomorphy for establishing a sister-group relationship; instead he considered the relationship of the Sabellariidae to other families still to be "obscure."

Hatschek (1893), in a brief but extremely influential paper, recognized the order Polychaeta, with, among others, the suborder Serpulimorpha, which contained the families Serpulidae (sabellids and serpulids) and Hermellidae. Orrhage (1980) suggested that recognition of these two groups within the same suborder followed from Meyer's (1888) views.

Although Hatschek provided no references, his phylogenetic tree (fig. 2) is similar to Meyer's "cladogram" in hypothesizing the Spionidae as giving rise to a number of groups, including the Serpulimorpha. Hatschek's system has been followed in various forms by a number of German and Scandinavian workers (e.g., Hempelmann, 1931; Friedrich, 1938; Hartmann-Schröder, 1971; Holthe, 1986).

Uschakov (1955) modified Hatschek's system somewhat in recognizing the order Serpuliformia, but moved the Sabellariidae (= Hermellidae) to the order Drilomorpha, which otherwise contained various other sedentariate families. Uschakov gave no explanation for this change. Benham (1896) appeared to follow Hatschek's (1893) order Polychaeta but divided the group into two "branches": Phanerocephala and Cryptocephala, the latter containing the suborders Sabelliformia and Hermelliformia.

In her work on the Pacific sabellids and serpulids, Bush (1905) proposed an odd system in which she separated the sabellids and serpulids into the tribes Sabellides and Serpulides. Within the Sabellides she recognized the families Sabellidae and Eriographidae, and in the Serpulides the family Serpulidae. Bush gave no reasons for this arrangement.

The last two major works which concerned the sabellid, serpulid, and sabellariid polychaetes were those of Rioja (1923) and Johansson (1927). Both workers appeared to follow Benham (1896) in recognizing the Sab-

elliformia and Hermelliformia. Johansson (1927) suggested that even if the terebellids (Terebelliformia) or sabellariids (Hermelliformia) are closely related to the sabelliforms, the presence of the branchial crown in the latter group was considered sufficiently strong to justify recognition of a distinct suborder.

Dales (1962) gave one of the earliest ordinal classifications based on explicit phylogenetic considerations. He placed the Sabellidae and Serpulidae into the order Sabellida and the Sabellariidae into the Spionida. The latter order also contained families such as the Spionidae, Chaetopteridae, etc. Dales suggested phylogenetic affinities between the sabellariids and other spioniforms because of similarities in larval form and origin of the palps. This classification has been reiterated by Dales (1963, 1977).

Clark (1969) essentially followed Dales' (1962) line of reasoning in allying the sabellariids with the spioniforms but used Hatschek's (1893) terminology for the orders (Spiomorpha and Serpulimorpha). In a synthesis of Dales' (1962) and Clark's (1969) ideas, Fauchald (1974) suggested an evolutionary scenario to explain the perceived adaptive radiation within the Polychaeta. Fauchald (1977) presented an ordinal classification based on these ideas. The majority of orders are of the form proposed by Dales (1962, 1963). Within the order Sabellida, Fauchald placed the Sabellidae, Serpulidae, Spirorbidae, and the recently described families Caobangiidae and Sabellongidae. Fauchald, however, moved the Sabellariidae to the order Terebellida, apparently to denote similarity of the enlarged anterior paleate setae in the Pectinariidae and Sabellariidae. Fauchald's (1977) ordinal arrangement of families has been widely recognized or, at least, inferred (e.g., Hobson and Banse, 1981; Pettibone, 1982; Uebelacker and Johnson, 1984; George and Hartmann-Schröder, 1985).

The latest change within the order Sabellida has been proposed by Knight-Jones (1981), suggesting that the Sabellariidae are most closely related to the sabelliforms. The basis for a relationship between these families is the presence of setal inversion. Holthe (1986) supported this view and suggested the

placement of the Sabellariidae in the Sabellida.

PROBLEMS WITH THE ORDER SABELLIDA

The adequacy of the Sabellida (including the Sabellariidae) as a group is here based on evidence of monophyly, i.e., that all families are more closely related to one another than to any other family, or at least definable on the basis of a unique, shared character. Such a character appears to be setal inversion. To understand the relations among the Sabellidae-Caobangiidae-Sabellongidae complex, the families as currently recognized are here considered to be inadequately defined. For any lower-level cladistic analysis, it is preferable to use as an outgroup a taxon which is considered to be monophyletic (Watrous and Wheeler, 1981; Wiley, 1981). Thus, the relationships of the families within the Sabellida must be discerned initially.

Figure 3 depicts a hypothesis of relationship based on current definitions of the families (e.g., Fauchald, 1977). The monophyletic status of the Sabellidae-Caobangiidae-Sabellongidae clade is not well established as seen by the apparent loss of thoracic uncini in the Caobangiidae (discussed below). The caobangiids do, however, possess the distinctive "cartilaginous" skeleton of many sabellid genera. There is a group of genera in the Sabellidae (*Fabricia*, *Fabriciola* Friedrich, *Augeneriella* Banse, *Manayunkia* Leidy) in which this skeleton is lacking. As a result, it is not known a priori if the absence of a skeleton is plesiomorphic or a secondary loss.

Giard (1893) recognized *Caobangia* as a member of the Sabellidae; subsequently a number of workers have assigned it to different subfamilies (e.g., Chamberlin, 1919; Zenkevitch, 1925; Hartman, 1951, 1959; Banse, 1957). In his work on this genus, Jones (1974a: 31) suggested placing it in a separate family for the following reasons: "1) the presence of neurosetal palmate hooks on the first setiger; 2) the absence of hooks of any sort on the following thoracic setigers; 3) the presence of two types of avicular hooks in the posterior region; and 4) the recurving of the gut within the body such that the anus opens

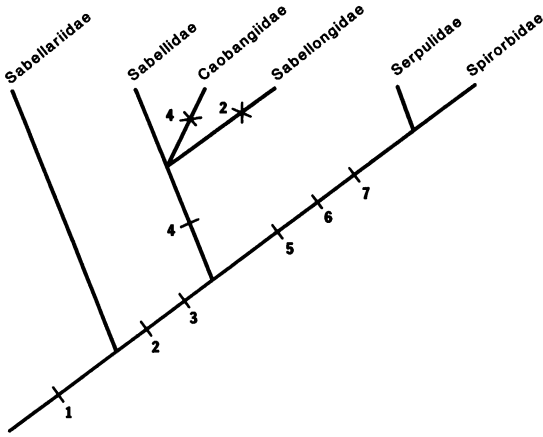


Fig. 3. Cladogram of relationships of families currently recognized in the order Sabellida (rooted using the Spionida as outgroup). Slashes on stems are synapomorphies, x's are reversals. Character changes are as follows: 1 = setal inversion, 2 = branchial crown, 3 = distinct inverted fecal groove, 4 = thoracic uncini with main fang and broad series of smaller teeth, 5 = tube calcareous, 6 = thoracic membrane, 7 = thoracic uncini saw-shaped or rasp-shaped.

far anteriorly." Additional characters cited for the new family were the placement of male and female gonopores and the presence of two pairs of nephrostomes.

The family Sabellongidae was erected by Hartman (1969) for the species *Sabellonga disjuncta* Hartman. Hartman justified separation of the species into a new family based on the apparent replacement of the branchial crown by a pair of grooved palps and the unusual falcate spines in the abdomen. She did, however, acknowledge the otherwise strong similarities the species has with a number of sabellid genera.

There appears to be no evidence to suggest that the caobangiids or sabellongids actually lie outside of the Sabellidae, i.e., that all Sabellidae genera are more closely related to one another than any one is to the caobangiids and/or sabellongids. The reasons given by Jones (1974a) and Hartman (1969) for erecting their respective families are only reiterations of generic-level characters; autapomorphies at this level provide no information at a higher level of generality to substantiate the view that the Sabellidae is not paraphyletic as a result of these changes. Even prior

to a cladistic analysis, I would consider it more parsimonious to suggest that the caobangiids belong in the Sabellidae on the basis of the common occurrence of the branchial skeleton, which may be primitively absent in some other sabellid genera. Likewise, *Sabellonga* displays companion setae, which are absent in many sabellid genera and remaining sabelliforms. By recognizing the Sabellongidae, the origin of companion setae is unnecessarily postulated to have arisen on at least two occasions. The trichotomy seen in figure 3 between the Sabellidae, Caobangiidae, and Sabellongidae, and the suspected paraphyletic nature of the Sabellidae is one of the primary objects of study in the present work.

If the Sabellidae-Caobangiidae-Sabellongidae clade can be considered to be monophyletic, then it appears that either the Serpulidae or Spirorbidae might act as outgroups. But before this can be done there must be evidence to support the hypothesis that each of these families is monophyletic. The serpulid subfamily Spirorbinae Chamberlin, 1919, was raised to the family level by Pillai (1970). The monophyletic status of this group appears to be well established in that spirorbids have an asymmetrical body and dextrally or sinistrally coiled calcareous tubes. Pillai also cited additional characters which distinguish serpulids from spirorbids; however, these are actually not synapomorphies for the Spirorbidae (Pillai, 1970: 144-145). Pillai's justification for the erection of the Spirorbidae is as follows:

... differences between spirorbids and the Serpulidae, therefore, outnumber the similarities and are of such magnitude as to justify the separation of spirorbids into a distinct family. The elevation of the Spirorbinae to the status of a Family, not only permits due recognition of a highly specialized group which have evolved from the Serpulidae and developed characters peculiar to themselves, but also obviates the difficulties hitherto encountered in their systematics and in obtaining a proper understanding of their phylogeny (Pillai, 1970: 145).

This elevation to family has been supported by various workers, e.g., Knight-Jones et al. (1975), Bailey-Brock and Knight-Jones (1977), Fauchald (1977), Knight-Jones (1978, 1981), and Orrhage (1980). Several recent workers still recognize the Spirorbinae (Hobson and Banse, 1981; ten Hove, 1984).

With the separation of the spirorbids, the

Serpulidae now contains three subfamilies: Filigraninae, Ficopomatinae, and Serpulinae (Fauchald, 1977). Traditionally, the filigranins have been characterized as either lacking an operculum or having one or more under-developed ones, whereas a well-developed operculum is present in the latter two subfamilies. The operculum of the Spirorbidae was considered as nonhomologous to that of serpulids by Pillai (1970) since the spirorbid operculum is always modified from the second, dorsalmost radiole on one side of the branchial crown, as opposed to the operculate serpulids, in which one of the first, dorsalmost radioles is always modified. The present relationships of the serpulid subfamilies and spirorbrids are presented in figure 4.

There are, however, several problems with this arrangement. ten Hove (1984) has shown that the serpulid operculum is actually a modified, *second*, dorsalmost radiole. It is only in large-bodied serpulid species that the opercular stalk migrates during development to a position which causes it to appear as though it originates as the first radiole. The operculum of small species can be readily observed as originating on the second radiole. The serpulid and spirorbid opercula appear to be homologous if the criterion of exact position is to be invoked, although this does not appear to be a strict requirement.

In accordance with figure 3, it would then be necessary to postulate loss of the operculum in the Filigraninae ancestor from an operculate serpulid-spirorbid ancestor. There is, however, no evidence, morphologically or ontogenetically, that such a loss has occurred in the serpulids (ten Hove, 1984). With the Sabellidae as a sister group, it would appear more informative to consider the lack of an operculum in some of the filigranins to be plesiomorphic. It must also be assumed that the calcareous tube of the serpulids is homologous to that of the spirorbrids such that there are two recognized states: straight (or irregular) and coiled. Again, parsimony would dictate that if the filigranins are the most plesiomorphic group of serpulids then the "straight tube" state would be plesiomorphic.

Based on the data at hand, there is no evidence to suggest that the operculate serpulids are all more closely related to one another

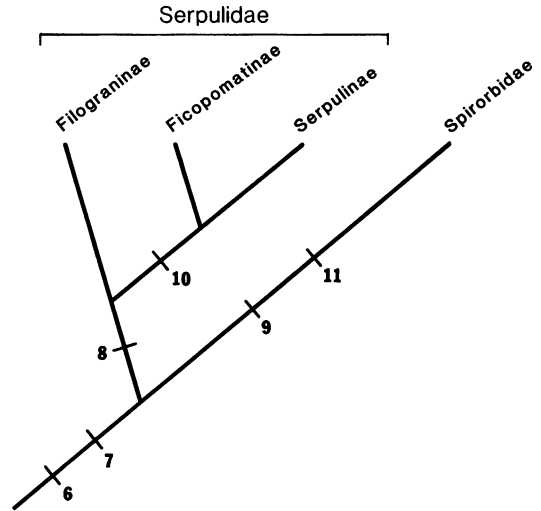


Fig. 4. Cladogram of relationships of the serpulid subfamilies and the Spirorbidae. See figure 3 for explanation of symbols. Character state changes for characters 6 and 7 are the same as in figure 3. Remaining character state changes are as follows: 8 = calcareous tube straight, 9 = calcareous tube coiled, 10 = operculum from radiole 1, 11 = operculum from radiole 2.

than any one is to the spirorbrids. In fact, Pillai (1970) noted that the spirorbrids probably evolved from a serpulid ancestor.

While the spirorbrids might form a monophyletic group, their separation from the Serpulidae results in the latter being paraphyletic. The justification for the Spirorbidae given by Pillai (1970; quoted above) actually reduces information on sister-group relationships and hypotheses of phylogenetic changes within the serpulid-spirorbid complex. I hereby suggest that the spirorbrids be placed back into the Serpulidae.

The relationship of the present Serpulidae s.l. subfamilies (including spirorbrids) is presented in figure 5. There do not appear to be any synapomorphies presently recognized for resolving the trichotomy among the operculate subfamilies. It appears, however, from information available in the literature, that the present serpulid subfamilies cannot be maintained. ten Hove (1984) has presented a hypothesis of sister-group relationships among the filigranin and some of the serpulid genera. Based primarily on a hypothesized transformation series from nonoperculate to operculate genera, he has shown that the Fil-

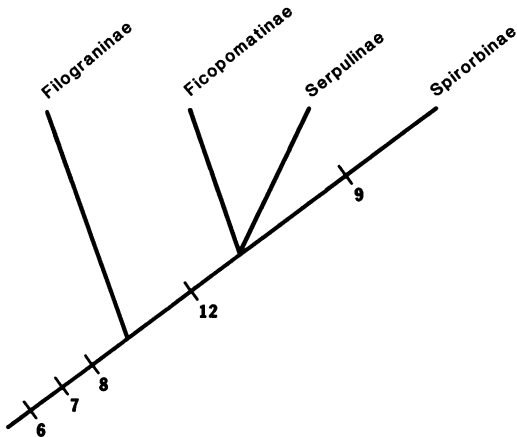


Fig. 5. Cladogram of relationships of the Serpulidae s.l. See figure 3 for explanation of symbols. Character state changes for characters 6–9 are the same as in figure 4. Remaining character state changes are as follows: 12 = operculum present.

ograninae is not a monophyletic grouping. In fact, the subfamily contains genera displaying a transformation from the nonoperculate condition (*Protula* Risso) through transitional operculate forms (*Salmacina* Claparède and *Filograna* Oken, fide ten Hove, 1984), with the more obvious operculate genera of the Serpulinae being a continuation of this grade. A more complete cladistic analysis of the Serpulidae will likely further indicate the untenable nature of these subfamilies.

Based on the above discussion, a partially revised pattern of relationships within the Sabellida is presented in figure 6. This pattern does not support the phylogenetic conclusions drawn by Knight-Jones (1981) concerning evolution within this group. Knight-Jones presented an adaptive evolutionary scenario for explaining various features within the Sabellida, especially as related to their tubicolous nature. Knight-Jones (1981: 197) suggested that the “archaic annelid” lived in soft sediments and may have resembled “*Manayunkia aestuarina* with its simple and relatively inefficient food gathering tentacles . . . or *Sabellonga disjuncta* with just two grooved appendages on each side of the mouth. . . .” Knight-Jones, however, considered these features in the above extant species to be secondarily derived. At some point in time, according to Knight-Jones (1981: 198), there would have been selective pressure for

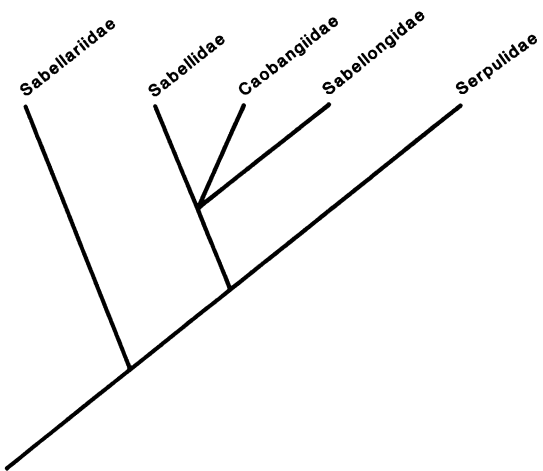


Fig. 6. Cladogram of relationships within the order Sabellida in which the Serpulidae s.l. is recognized.

settling on elevated, hard substrates and development of the ability to secrete coiled calcium carbonate tubes: “It seems that all sabelliform families were derived from sinistrally coiled ancestors.” Although Knight-Jones did not cite Meyer (1888), their views closely parallel one another in this regard. As indicated by the present cladogram (fig. 6), there are no data to support the above claims. Knight-Jones also suggested that the Sabellidae and Caobangiidae are “recently evolved” or “young” families because of great morphological and physiological diversity. In addition, the Sabellidae appear to “occupy a central position in the order, and perhaps an advanced position.” The nature of “recently evolved” or “advanced” in the above contexts is ambiguous in denoting patterns of relationship, especially given the questionable status of the Sabellidae as a monophyletic group.

As noted earlier, the present sister-group relations of the Sabellariidae, Sabellidae-Caobangiidae-Sabellongidae complex, and Serpulidae are based on the presence of setal inversion. In addition, various workers have noted similarities between the palps of sabellariids and various spioniform groups. Dales (1962, 1963) suggested a closer relationship between the spionids, chaetopterids, and sabellariids due to the similar structure of the palps. The histological studies of sabellariid palps by Orrhage (1978) have shown these

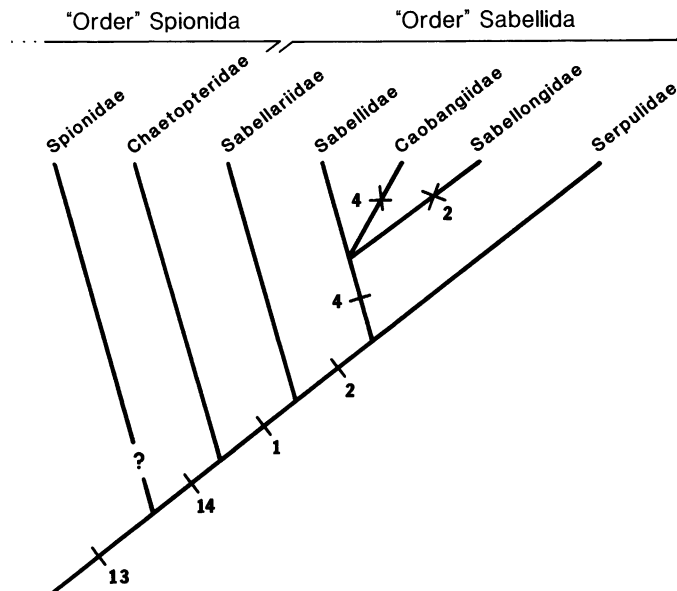


Fig. 7. Cladogram of possible relationships of families of the orders Sabellida and Spionida. Spionida is paraphyletic as a result of recognizing the Sabellida. See figure 3 for explanation of symbols. Character state changes for characters 1, 2, and 4 are the same as in figure 3. Remaining character state changes are as follows: 13 = grooved palps, 14 = abdominal uncini saw-shaped or rasp-shaped.

organs to be homologous to the grooved palps of such spioniforms as the Spionidae, Trochochaetidae, Poecilochaetidae, Chaetopteridae, Flabelligeridae, and Magelonidae (Orrhage, 1964, 1966, 1974). Orrhage (1980) has determined that the branchial crown of the Sabellidae and Serpulidae is homologous to the palps of the above spioniform families.

The somewhat opposing views of Meyer (1888) and Dales (1962, 1963) may now be reconciled. The specific criticism (discussed above) by Orrhage (1980) of Meyer's (1888) evidence for a close relationship between the Sabellariidae and Sabellidae-Serpulidae clade is legitimate, but does not falsify the general pattern of relationship Meyer suggested. It appears that Dales' independent, or implied monophyletic, lineage concepts of the Spionida and Sabellida are incorrect. The homology of grooved palps in the Sabellariidae and the Spionida would indicate that at the very least the Spionida is paraphyletic (fig. 7). At this point it is probably only worthwhile to recognize a "spionida" group of families which possess grooved, ciliated palps, and to which should be added the sabelliform families. Contrary to Dales' (1963) view, the saw-shaped or pectinate uncini of the Chaetopteridae may indicate this family is the sister group to the sabelliforms, especially in conjunction with the presence of palps (fig. 7).

In addition, the above "spionida-sabellida" cladogram (fig. 7) may not be accurate insofar as it does not include the terebellomorphs: Pectinariidae, Ampharetidae, Alvinellidae, Terebellidae, and Trichobranchidae. Holthe (1986) recognized the order Terebellomorpha (or Terebellida) for these families: this arrangement differs little from previous ones. The only autapomorphies defining this order are the numerous tentacles which extend from the peristomium and the paired branchiae located on several anterior thoracic setigers. It is assumed that loss of either of these characters in the order is secondary. The terebellomorphs also display uncini which are very similar to those of the sabelliforms; however, the degree of plasticity of uncini may preclude relying on them as the only character for establishing relationships at this level. Holthe (1986) did imply a possible sister-group relationship of the terebellomorphs to the Maldanidae based upon similarities of uncini. An additional character may be the tentacles.

Orrhage (1978) noted that the tentacles of the Sabellariidae are extensions of the upper lip; thus, they would be peristomial in origin. Day (1967) pointed out that the "buccal" tentacles of the terebellomorphs are extensions of the two upper lips, and of stomodeal origin. Holthe (1986) suggested that terebellomorph tentacles may have been derived from "pharyngeal papillae." This implies that the present position of the tentacles on the upper lips is in fact peristomial, contradicting Dales' (1962, 1963) view of a prostomial origin of the tentacles. Apparently no histological or developmental studies have been conducted to determine homology of these structures between the two groups.

If the terebellomorphs are part of the

Spionida group then they are also defined by the loss of palps or by rudiments if such can be found histologically. The fact that the terebellomorphs do not display setal inversion makes it difficult to place them into the Spionida group based only upon the presence of oral tentacles. Such an arrangement would necessitate either the reversal of setal inversion in the terebellomorphs, loss of oral tentacles in the sabellids and serpulids, or the homoplasious origin of oral tentacles. Holthe (1986) has stated that the enlarged paleate setae of the Pectinariidae are notopodial in origin; the degree to which these setae are homologous to those of the Sabellariidae might also need to be taken into account before this problem is considered further.

THE SABELLIDAE SUBFAMILIES

The distribution of sabellid genera within subfamilies has varied, depending primarily upon defining criteria favored, with little attention to phylogenetic or strictly systematic considerations. Chamberlin (1919) was the first to designate subfamilies, segregating *Caobangia* into the Caobangiinae [sic] while retaining all other genera in the nominal subfamily, Sabellinae. This arrangement has never been used by any other worker.

Rioja (1923) divided the sabellids into three subfamilies based primarily on setal characters. The Sabellinae contained those genera with (1) avicular thoracic uncini, which may have a prolonged base; (2) companion setae usually present; (3) a distinct fecal groove; and (4) well-developed ventral shields. The subfamily Fabricinae [sic] was defined to include genera in which the thoracic uncini have "long stems" (acicular). The Myxicolinae, containing only *Myxicola*, are distinguished by the presence of (1) radioles united for most of their length by a palmate membrane; (2) abdominal uncinal tori forming almost complete cinctures; and (3) a transparent, gelatinous tube. Note that the character set used by Rioja is not entirely consistent in all three subfamilies he defined.

Zenkevitch (1925) suggested dividing the sabellids into two subtribes: Thoracogoneata and Abdominogoneata. Thoracogoneata was

defined for genera in which gametes develop in thoracic segments and are discharged via modified nephridial ducts (gonoducts) into a common duct which opens far anteriorly. Abdominogoneata contained genera in which gametes develop in abdominal segments, with segmental abdominal gonoducts modified from nephridia, and abdominal gonopores. The genera listed by Zenkevitch within the Thoracogoneata correspond to Rioja's (1923) Fabricinae, except that *Jasmineira* was referred to the Abdominogoneata. *Myxicola* was placed within the Abdominogoneata, with remaining genera corresponding to Rioja's (1923) Sabellinae.

Johansson (1927) modified Rioja's (1923) subfamily arrangement by placing *Myxicola* into the revised subfamily Fabriciinae [sic]. Johansson defined the Sabellinae by (1) the occurrence of short-handled uncini in both the thorax and abdomen; (2) longitudinal muscle cells not being "nematoid"; (3) the branchial crown being innervated by only one pair of nerves; and (4) lacking special sense organs ("Flimmerorgane"). According to Johansson, the Fabriciinae had (1) long-handled uncini at least in the thorax; (2) longitudinal musculature usually "nematoid"; (3) innervation of the branchial crown by two pairs of nerves; and (4) special sense organs. Banse (1957, 1970, 1972) incorporated ele-

ments of Zenkevitsch's (1925) definitions into Johansson's subfamily scheme by recognizing the thoracogoneate and abdominogoneate fabriciins, and abdominogoneate sabellins (also see below).

Fauchald (1972) narrowed Rioja's (1923) definition of the Sabellinae to contain only genera in which companion setae were present; the Fabriciinae contained only genera without companion setae, but with short abdominal uncinigerous tori. Fauchald recognized the Myxicolinae, with *Myxicola*, as that group without companion setae but in which abdominal tori form nearly complete cinctures. Fauchald noted that his definitions would necessitate moving some genera, e.g., *Branchiomma* Kölliker, from the Sabellinae to the Fabriciinae. He considered this necessary in order to produce more well-defined categories. Fauchald later (1977) changed his mind, however, and assigned genera according to Rioja's definitions.

In a description of a new genus, *Pseudofabricia*, Cantone (1972) recommended the placement of *P. aberrans* in a new subfamily, Pseudofabriciinae. The distinctive nature of the collar, which differed from that seen in fabriciins, and the lack of a branchial crown were used as defining features for Cantone's subfamily. The subfamily Pseudofabriciinae has apparently not been recognized by other workers. Further, based upon the original description, I believe Cantone's taxonomic conclusions are in error. Examination of more material from the type locality will probably reveal that loss of the branchial crown is simply a fixation artifact. The specimens do possess a pair of eyes in the peristomium and a pair of pygidial eyes. Fauchald (1977) incorrectly diagnosed the genus as having a branchial crown with eight pairs of radioles.

SYSTEMATIC STUDIES OF THE SABELLIDAE SUBFAMILIES AND GENERA

The most widely accepted subfamily arrangement has been that of Rioja (1923; e.g., Fauvel, 1927; Hartman, 1951, 1959; Hartmann-Schröder, 1971; Fauchald, 1977; Orhage, 1980; Knight-Jones, 1981; Pettibone, 1982), while that of Johansson (1927) has been used infrequently or in a modified ver-

sion (e.g., Day, 1967; Banse, 1957, in part). General acceptance of Rioja's scheme appears to have been one of convenience, with little attention to phylogenetic or systematic considerations.

The groupings discussed by Meyer [1888: Sabellidae, Eriographidae (*Myxicola*), Amphicoridae (*Fabricia*)], based on explicit phylogenetic considerations, are similar to the subfamily groupings of Rioja. Meyer considered the Sabellidae to be the most plesiomorphic group; the eriographids and amphicorinids were characterized as apomorphic sister taxa (fig. 8A). The primitive nature of the sabellids was denoted by their sessile nature and well-developed collar, with these features present in the sabellid-serpulid ancestor. Meyer considered the eriographids and amphicorinids to be more derived on the basis of the loss of the ventral lips, the reduction of the collar to a ventral projection, and their more motile nature. Meyer viewed the increased motility of these two latter groups as a convergence with the free-living serpulacean ancestor.

Rioja later treated his original (1923) subfamilies in a phylogenetic context (Rioja, 1929, 1931). Rioja's views on which subfamilies are primitive and derived differed from those of Meyer (1888); however, the criterion for assessing polarity was still along the same lines. The primitive features, according to Rioja, should occur in relation to the errant lifestyle in certain groups of genera, reflecting maintenance of the ancestral condition. Thus, he (1929, 1931) suggested that the Myxicolinae were most primitive, followed by the Fabricinae, with the Sabellinae being most derived (fig. 8B).

Those characters which were considered primitive included pygidial eyes, the tendency for otocysts to be present, a rudimentary collar (or its loss), and poor development of the ventral shields. Rioja noted that there was a trend toward decreasing motility in the Fabricinae in association with loss or changes in the above characters. Members of the most advanced subfamily, Sabellinae, were for the most part sessile. Rioja placed considerable importance on setal forms; the simple limbate condition of the Myxicolinae and some Fabricinae was considered primitive while the Sabellinae displayed far more differentiation.

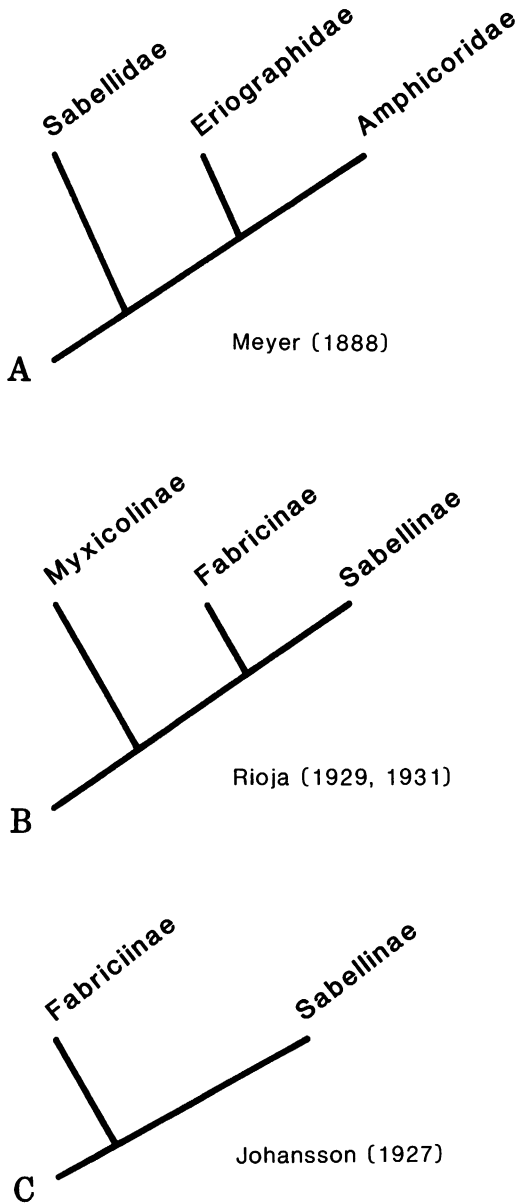


Fig. 8. A. Summary cladogram of phylogenetic relationships suggested by Meyer (1888) for the then recognized sabelliform groups. B. Summary cladogram of phylogenetic relationships suggested by Rioja (1929, 1931) for the sabellid subfamilies. C. Summary cladogram of phylogenetic relationships suggested by Johansson (1927) for the sabellid subfamilies.

The uncini of the Myxicolinae were thought to resemble most closely those of some members of the terebellomorph families Terebellidae and Trichobranchidae. Similar uncini

are also present in some Fabricinae. The uncini of the Sabellinae were considered the most derived state in that the avicular form was most common.

In modifying Rioja's (1923) subfamily scheme, Johansson (1927) justified placing *Myxicola* into his Fabriciinae because it had the defining qualities of the group (discussed above; fig. 8C). Johansson viewed the Fabriciinae as most primitive because of the occurrence of "nematoid" longitudinal muscle cells. Orrhage (1980) has pointed out errors in Johansson's scheme, i.e., the widespread nature of nematoid musculature, the lack of a difference in branchial nerve innervation between the subfamilies, and the occurrence of special sense organs in both subfamilies. Orrhage (1980: 162) supported the three-subfamily scheme of Rioja (1923), adding that "it may be said that Rioja's division of the Sabellids into three subfamilies of his seems to reflect a phylogenetic reality and that the reasons given by Johansson for unifying the Fabriciinae and Myxicolinae into one subfamily are not valid."

While Orrhage (1980) was justified in criticizing Johansson (1927) for the introduction of certain characters of dubious value at the subfamily level, he neglected to note that Johansson recognized the same basic differences in thoracic uncini used by Rioja (1923) in defining his subfamilies. Johansson apparently attempted to redefine subfamilies in a manner that would produce as much within-taxon consistency as possible. Johansson's decision to place *Myxicola* in the Fabriciinae is justifiable from the standpoint that he attempted to emphasize the similarities of other fabriciina genera (s.s.) with *Myxicola*, as opposed to pointing out uniquely derived characters of the latter, which would be uninformative as subfamily characters. From this point of view, Johansson's scheme is more successful than Rioja's in attempting to "reflect a phylogenetic reality" since it comes closest to considering taxonomic groups in terms of monophyly. Orrhage's acceptance of Rioja's scheme appears based not so much on a desire to accurately reflect phylogeny and/or sister-group relationships as it is to support paraphyletic groupings, i.e., stressing the odd nature of *Myxicola* as opposed to its relationship to other genera.

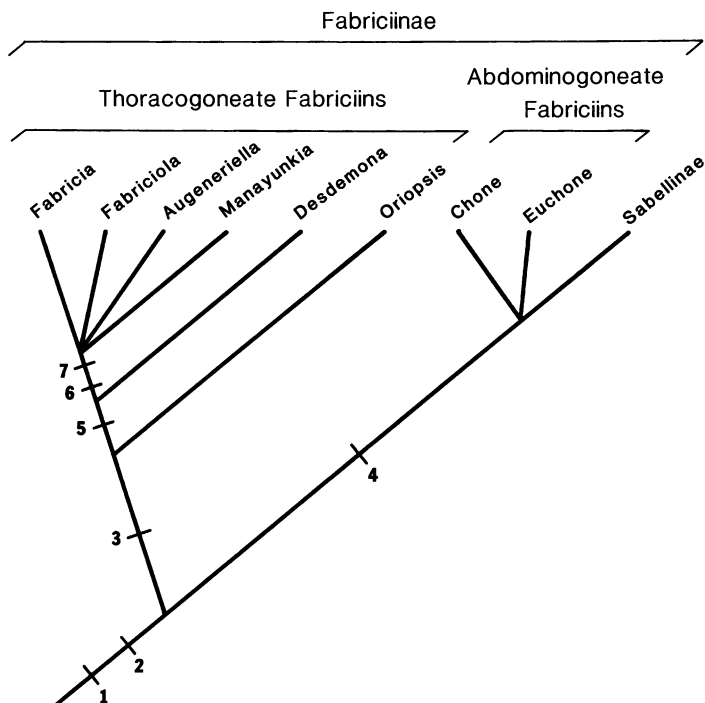


Fig. 9. Cladogram summarizing phylogenetic relationships and groupings discussed by Banse (1957, 1970) for selected members of the Sabellidae. See figure 3 for explanation of symbols. Character state changes are as follows: 1 = abdominogoneate, 2 = pinnules of unequal length, 3 = thoracogoneate, 4 = pinnules of equal length, 5 = three pairs of radioles, 6 = abdominal uncini with long manubrium, 7 = branchial hearts.

Explicit considerations of generic-level phylogenetic relationships have been limited. In his work on fabriciine genera, Banse (1957, 1970) has considered relationship to some extent. Banse has agreed with Johansson that, as a group, the Fabriciinae (sensu Johansson, 1927) are more primitive than the Sabellinae. In addition, Banse recognized the subgrouping of fabriciine genera as thoracogoneate or abdominogoneate (sensu Zenkevitch, 1925). The abdominogoneate condition was considered primitive since it occurred in the Serpulidae. Further, the presence of rasp-shaped uncini (sensu ten Hove, 1984) was considered the primitive uncinial condition for essentially the same reason. My interpretation of Banse's (1957, 1970) views are summarized in a cladogram (fig. 9).

Banse considered the ancestral sabellid to be "between" the *Oriopsis*-*Chone* evolutionary lineages. The *Oriopsis* group contained the thoracogoneate fabriciins, with *Oriopsis* Caullery and Mesnil the most primitive ge-

nus of the clade on the basis of having radiolar pinnulae of unequal length, more than three pairs of radioles and more than three abdominal setigers. *Desdemona* Banse was placed between *Oriopsis* and the *Fabricia*-*Fabriciola*-*Augeneriella*-*Manayunkia* group on the basis of possessing only three pairs of radioles as seen in the latter group of genera. Banse (1957) appeared inclined to view the ancestral sabellid as looking very much like *Oriopsis*. In being thoracogoneate, however, *Oriopsis* was considered to have shown divergence from this primitive form. Because of this derived condition, Banse disagreed with Rioja's (1929) view that the errant fabriciins per se (e.g., *Oriopsis*, *Fabricia*) were representative of the ancestral condition (i.e., plesiomorphic to remaining sabellids). Similar disagreement was met in relation to the absence of a collar as a primitive feature. The most primitive of the abdominogoneate fabriciins should be *Chone* Kröyer or *Euchone* Malmgren, according to Banse (1957, 1970),

since in some species the abdominal rasp-shaped uncinial form still occurs. Divergence from the ancestral condition has also occurred relative to the pinnulae, which is of equal length throughout. Banse (1970) also noted that, in at least one species of *Euchone* (*E. hancocki* Banse) the thoracogoneate condition might be present. The implications of this observation to the above phylogenetic scheme were not pursued explicitly but, in

general, convergence as a result of small size was suggested.

Based upon Banse's (1957, 1970) phylogenetic views, it is interesting to note the apparent paraphyletic nature of the Fabriciinae (fig. 9). Banse appears to be one of the few workers to have recognized that the fabriciina genera represent, at least to an extent, only a part of the overall sabellid clade which ultimately leads to the Sabellinae genera.

CLADISTIC ANALYSIS OF GENERA IN THE SABELLIDAE-CAOBANGIIDAE-SABELLONGIDAE COMPLEX

SELECTION OF INGROUP AND OUTGROUP TAXA

For the present analysis, 34 genera were included from the Sabellidae, as well as the caobangiid and sabellongid genera, *Caobangia* and *Sabellonga*, respectively. Appendix I lists all species examined, the necessary references for identification of the specimens examined, and literature sources used to supplement study of preserved material. The majority of these genera are those recognized by Fauchald (1977), except for changes resulting from the recent revisions of Knight-Jones (1983), Perkins (1984), and Perkins and Knight-Jones (in press).

Some genera were not included for taxonomic reasons or due to unavailable or incomplete material (as specified below). *Euratelletta* Chamberlin, 1919, was incompletely described and no material was available. *Pseudofabricia* Cantone was described from incomplete specimens (see subfamily review above) and is probably a species of *Fabricia*. *Brandtika* Jones, 1974b, was described from dried material and most features of the branchial crown are unknown. *Monroika* Hartman, 1951 (type species: *Manayunkia africana* Monro, 1939) could not be obtained from the British Museum (Natural History) in time to be included in the study.

The genus *Dialychone* Claparède, 1870, was not included since, in part, type material for *D. acustica* does not exist. The only supposed character separating this genus from *Chone* is the lack of a palmate membrane in the former. A specimen (provided by Dr. Ad-

riana Giangrande, Università di Pisa) identified as *D. acustica* from near the type locality (along the coast near Naples) was found to possess a low palmate membrane. For this study, *Dialychone* is considered a synonym of *Chone*.

The genus *Euchonella* Fauchald, 1972, with *E. magna* the only species, is considered a synonym of *Euchone*. The holotype possesses an anal depression like that of *Euchone*. Contrary to Fauchald's description, a palmate membrane is present and the anal depression is ventral. The depression is bordered by a thickened rim which is continuous anteriorly; it does not display the horseshoe-shaped plaque described by Fauchald.

Distylidia Hartman, 1961, was synonymized with *Demonax* Kinberg, 1867, by Perkins (1984) and *Spirographis* Viviani, 1805, is now considered a synonym of *Sabella* Linnaeus, 1767, according to Perkins and Knight-Jones (in press). *Chone* Kröyer, 1856, was split into two groups for the present analysis on the basis of certain characters discussed in detail below.

Because of the large numbers of genera and species within the Sabellidae, and the obvious need for revisions at the specific level (e.g., Knight-Jones, 1983; Perkins, 1984), the species used in the present study were restricted primarily to the type species of each genus. In instances where obvious interspecific variability occurred in recognized supraspecific characters, additional species were examined to determine the usefulness of the character at hand. Material examined usually included type material and/or type species

which had been collected as close to the type locality as possible. In addition, original descriptions were consulted.

The polarization of character states (i.e., determination of plesiomorphic and apomorphic transformation series) was determined by outgroup comparison (Hennig, 1966; Wiley, 1981; Watrous and Wheeler, 1981). Based upon the arguments presented above, the outgroup for the present study was the Serpulidae s.l. Initially, *Protula* was considered to have representative character states of the serpulids since ten Hove (1984) recognized it as the most plesiomorphic serpulid genus. Examination of non-"filigranin" genera was undertaken to determine the degree to which character states differed within the Serpulidae. Further considerations of character state polarization are discussed below.

CHARACTER SELECTION AND CHARACTER STATE TRANSFORMATION SERIES

As many characters as possible that appeared to be consistent at the generic level were included in this analysis. No a priori character weighting was used. The majority of characters can be considered those which have been "traditional" in sabellid taxonomy. Recently, Knight-Jones (1983) and Perkins (1984) have incorporated additional, usually undescribed characters, e.g., branchial crown skeletal structure, aspects of dorsal lip construction, and greater attention to thoracic notosetal forms and distribution. These characters, as well as several previously overlooked characters, have been included. In the past, most of these newly recognized characters have been described only vaguely, if at all.

Forty-three morphological characters were used in the study. Appendix II contains a listing of characters and associated states. The majority of characters have binary states (presence/absence). Multistate characters in Appendix II are presented in an unordered series, as applied in the cladistic analysis (see below). The following discussion examines characters, or suites of characters, used in the analysis and the manner in which character states manifest themselves.

Sabellids have several distinct regions (fig.

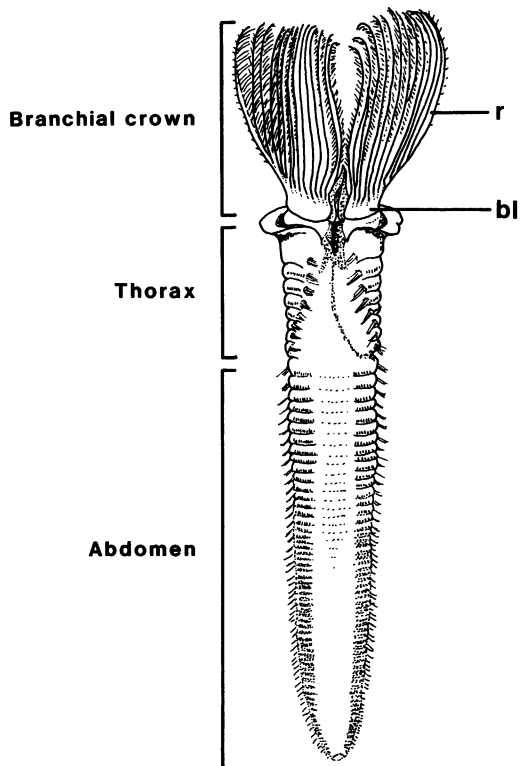


Fig. 10. Dorsal view of *Branchiomma violacea* (Schmarda) (after Day, 1967). Major body regions from which characters were examined are indicated.

10). Discussion of the different characters is related to these different body regions. Arabic numerals (1 through 43) and associated letters (e.g., state 4c) used below refer to characters and states, respectively, listed in Appendix II. In all instances, state "a" is considered plesiomorphic and states "b", "c", etc., as apomorphic.

CHARACTERS OF THE BRANCHIAL CROWN

The branchial crown of sabellids is composed primarily of two structural components: branchial lobes (sensu Nicol, 1931) and radioles (bl, r, fig. 10). The branchial lobes are the proximalmost part of the crown and are attached to the anterior end of the body. The lobes are located in a lateral position on either side of the mouth and are slightly curved such that they are concave in cross section relative to the mouth. A variable

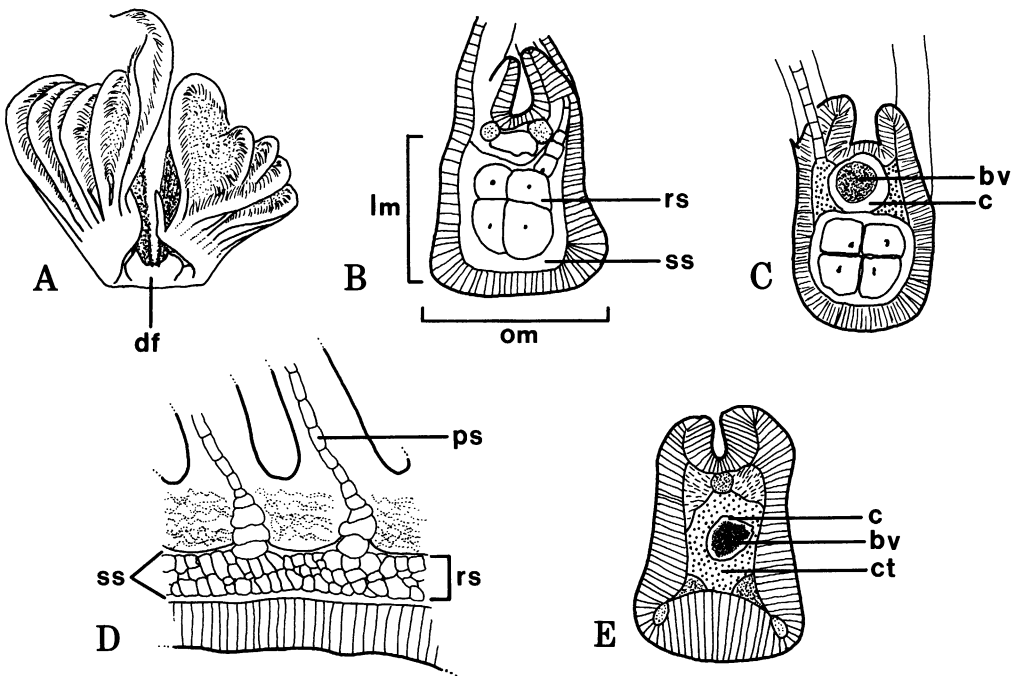


Fig. 11. A. Branchial crown (ventral view) of *Demonax krusensterni* Kinberg, showing U-shaped configuration of branchial lobes and dorsal fusion (after Knight-Jones, 1983). B. Cross section of radiole (proximal region) of *Hypsicomus stichophthalmos* Grube (after Perkins, 1984). C. Cross section of radiole (median region) of *Sabella pavonina* Savigny (USNM 19618). D. Sagittal view of radiole of *Demonax microphthalmus* (Verrill), illustrating radiolar and pinnular skeletal axis cells (after Perkins, 1984). E. Cross section of radiole of the serpulid *Pomatoceros triqueter* (Linnaeus) (after Thomas, 1940).

number of radioles are attached along the distal margins of the lobes.

Along the inner margins of each radiole are a paired series of ciliated pinnules, beginning just distal to the radiole base and extending to near the radiole tip. Each pinnule within a pair lies slightly oblique to the other. Pinnule length may vary such that the proximalmost pinnules extend to the end of the crown and more distal pinnules become successively shorter, resulting in all pinnules terminating at the distal end of the crown. In other taxa, pinnule length is uniform over the entire radiole. The pattern of pinnule length is usually consistent within a genus except in cases where interspecific size varies markedly (e.g., *Chone* and *Euchone*), in which very small species display the former condition and larger species the latter.

Descriptive accounts of branchial crown morphology have been given by Claparède (1873), Nicol (1931), and Thomas (1940).

Evidence of homology of the branchial crown and comparisons of some detailed structures between the Sabellidae and Serpulidae have been provided by Orrhage (1980).

The branchial lobes may be completely separate from one another (state 1a; e.g., *Manayunkia*, *Fabricia*), or the dorsal margins may be fused (state 1b; e.g., *Chone*, *Sabella*), giving the entire structure a U-shaped appearance (df, fig. 11A). Within the Serpulidae, the dorsal margins of the lobes always appear separate. In some specimens, however, the ventral margins do appear to be fused just ventral to the mouth; ventral fusion is never present in sabellids.

The external surface of the radioles, primarily on the lateral and outer margins, and on the pinnules, may be smooth (state 2a; e.g., *Fabricia*, *Sabella*, *Oriopsis*) or have minute folds or wrinkles (state 2b; e.g., *Manayunkia*, Genus A). The wrinkled appearance may be due to the formation of folds or ridges

on the epithelial surface. These wrinkles are generally oriented perpendicular to the long axis of the radioles or pinnules. While consistency of this character appears to be good, its manifestation in preserved material may in fact be an artifact of contraction. This, however, would not negate the use of such a quality as a character.

Cross sections of the radioles may be distinctly quadrangular (state 3a; fig. 11B), or outer and lateral margins may not be distinct, making the outer radiolar surface appear rounded (state 3b; fig. 11C). The rounded condition was noted in *Eudistylia* and *Schizobranchia* by Bush (1905), and in *Sabella* by Perkins and Knight-Jones (in press). My inclusion of this condition in this analysis is still questionable since it is sometimes difficult to accurately discern these states. In genera which appear to lack a branchial skeleton (discussed below), the cross section of the radioles is more depressed or flattened (state 3c), with only the inner and outer margins distinct. Only recently has the shape of radiolar margins been examined in a consistent manner (e.g., Knight-Jones, 1983; Perkins, 1984).

In forms in which the branchial lobes are fused dorsally, a branchial skeleton is present. The skeletal tissue is composed of large, thick-walled cells, each with a large fluid-filled vacuole surrounded by a supporting sheath of hyaline material interspersed with anastomosing cells (rs, ss, fig. 11B, C). As noted by Nicol (1931), the skeletal tissue is not homologous to cartilage as is implied by the terminology used in most taxonomic studies. The supporting sheath contains cells and, unlike cartilage, is separable from the large, vacuolated cells (Viallanes, 1885). Krukenberg (1881) found no similarity in chemical composition to indicate homology between this tissue and that of vertebrate cartilage. Thus, Nicol (1931) preferred to call the structures formed from the two cell types "supporting axis" and "sheath," respectively. Thomas (1940) used the terms "skeletal axis" and "skeletal sheath." Fitzharris (1976) examined the histochemical makeup of this region from *Sabella* (= *Bispira*) *melanostigma* Schmarda. He noted that the supporting sheath ("basement membrane") has the fibrous consistency of collagen, with much of

this material being removed upon treatment with collagenase. Fitzharris did, however, find that there is a very thin layer of material surrounding the skeletal axis cells ("chondrocytes") which is similar to matrix produced by vertebrate cartilage cells.

The branchial skeleton extends into each branchial lobe as basal lamellae (sensu Nicol, 1931) connected together dorsally by a narrow transverse bar. This basal region of the skeleton conforms to the general U-shaped configuration of the branchial lobes (fig. 11A).

From the anterior margins of the basal lamellae are skeletal outgrowths, each referred to as a radiolar skeleton, which extends through the long axis of each radiole (rs, fig. 11B, D) and into the pinnules. The skeletal axis cells in a radiole may be arranged in a single row (state 4d), composed of two rows (state 4c), or four or more rows, or irregular groups, of cells (state 4b). The cells tend to be wider than long. In radioles with two rows, the cell pairs lie side by side with the longest axis in cross section extending toward the lateral margins of the radiole. In radioles with four rows, the cells form a quadrangular unit in cross section, whereas in radioles with more than four cells the arrangement is often completely irregular.

While the arrangement of skeletal axis cells in the radioles has been discussed in morphological works (e.g., Claparède, 1873; Nicol, 1931; Thomas, 1940), its application in systematic studies has been limited. Knight-Jones (1983) and Perkins (1984) have illustrated the cross-sectional arrangement of these cells but did not attribute any definite systematic importance to their arrangement at the generic level.

In the present study, examination of the skeletal axis cells was made primarily in the median region of a radiole. Variability in numbers of cells over the length of the radiole occurs most widely in taxa with four or more rows of cells but does not alter the nature of this character state. In most genera, however, the number of rows of cells decreases to two or one near the extreme distal ends of radioles. Thus, the median region of radioles usually displays greatest consistency within a given genus.

Skeletal axis cells extend into the pinnules as a single row, usually being longer than wide

(ps, fig. 11D). In most cases, the one to two proximalmost cells, which are adjacent to the radiolar skeleton, tend to be somewhat larger than remaining distal cells. No consistent systematic differences appear present in the pinnular axis cells of the different genera.

A branchial skeleton is absent (state 4a) in the Serpulidae, this region being filled with connective tissue (ct, fig. 11E; Thomas, 1940). Rioja (1929) viewed the presence of a branchial skeleton as a primitive feature since it was reported present in the serpulid *Josephella* by Caullery and Mesnil (1896). Careful examination of specimens of this genus reveals the absence of a skeleton. It is likely that Caullery and Mesnil misinterpreted the presence of connective tissue in this region since it tends to be broken up into what appear to be skeletal elements.

A branchial skeleton is apparently also absent in some sabellid genera (*Manayunkia*, *Fabricia*, *Fabriciolo*, *Augeneriella*). This phenomenon has apparently not been noted in most works on this group (e.g., Zenkevitch, 1925; Banse, 1956) and has not been incorporated as a systematic character. Although Hartmann-Schröder (1986) did mention that a skeleton is lacking in *Fabriciolo* and *Augeneriella*, no reference was made to past works. In a study of feeding and tube-building behavior in *Fabricia sabella* (Ehrenberg) and *Manayunkia aestuarina* (Bourne), Lewis (1968: fig. 1c) illustrated a cross section of a radiole of *Fabricia*. The figure has a circular area labeled "cartilage" which appears to depict a single skeletal cell. Interpretation of this structure as a skeletal element is dubious since no indication of typical skeletal cell structure can be discerned. Lewis (1968: fig. 1e) also figured a cross section of a pinnule of *Manayunkia*; no skeletal cells are indicated [see also Zenkevitch, 1925, for *M. baicalensis* (Nusbaum)]. It does not appear as though any detailed histological studies have been made to determine if the arrangement of radiolar tissues and coelom is similar to that of serpulids.

A pair of structures commonly referred to as branchial hearts is found in genera which lack a branchial skeleton (state 5b; bh, fig. 14D, E). The branchial hearts are roughly circular chambers situated in each branchial lobe, near the dorsal margins. The hearts are

joined by a blood vessel extending from the thorax; this vessel, according to Schmidt (1848), connects the thoracic vascular loops to the branchial hearts. Another vessel has been reported connected to the hearts in *Manayunkia*, which extends into the ventral filamentous appendages (Banse, 1956; discussed below). A similar connection has been observed in the undescribed fabriciini genus, Genus A. Leidy (1883) did not identify branchial hearts in *M. speciosa* Leidy but did illustrate the extension of a pair of blood vessels from the thorax into the branchial crown. In the branchial lobes, the vessels form a distinct bend before extending into the ventral filamentous appendages. Leidy's interpretation of this bend is in all probability a representation of the branchial hearts. Various workers have noted pulsations in the hearts (e.g., Ehrenberg, 1836; Claparède, 1862; Langerhans, 1881; Verrill, 1873; McIntosh, 1923). The branchial hearts have been afforded minor systematic recognition in the past, usually for grouping some genera in a general sense only.

Distal to the branchial lobes, the radioles may be completely separate (state 6a) or joined for part of their length by a palmate membrane (state 6b; pm, figs. 12B, 14A). The palmate membrane in sabellids is an extension of the lateral sides of two adjacent radioles (pm, fig. 12A) and is covered on both sides by columnar epithelium, between which is a layer of skeletal sheath material (Nicol, 1931; Orrhage, 1980; Perkins, 1984). Recognition of the palmate membrane may be arbitrary in some instances; in some genera which have been reported not to possess a palmate membrane, there may be a very low membrane connecting the radioles just as they extend from the branchial lobes. Thus, the presence of a palmate membrane has traditionally been denoted by the well-developed nature of the structure along the radioles.

The membrane appears to be a consistent generic character except in *Euchone*, where it has been reported absent in some small species (Banse, 1970); in these cases the membrane may be present but very low. Further, a palmate membrane might not be present in all species of *Potamilla* Malmgren (T. H. Perkins, personal commun.).

The radiolar flanges (state 7b), which usu-

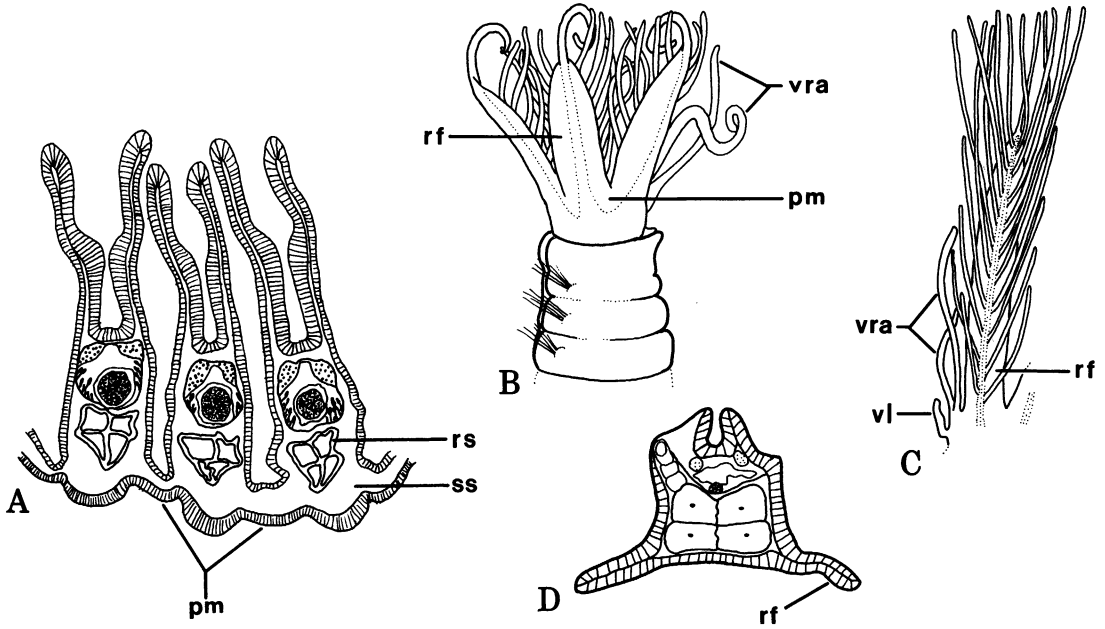


Fig. 12. A. Cross section of three radioles (proximal region) of *Sabella pavonina* Savigny joined together by a palmate membrane (after Nicol, 1931). B. Anterior end (lateral view) of *Oriopsis ehlersi* Day (after Day, 1967). C. Ventralmost region of right branchial lobe (inner margin) of *Oriopsis armandi* (Claparède) (after Banse, 1957). D. Cross section of radiole (median region) of *Notaulax paucoculata* Perkins (after Perkins, 1984).

ally extend from the outer corners of the radioles (rf, fig. 12B, C), resemble the palmate membrane in structure. They may be composed of only two layers of columnar epithelial cells or the skeletal sheath may also be present (rf, fig. 12D). In the far distal regions of the radioles of some species the axial skeleton may also extend into the flanges (Perkins, 1984). Flanges may or may not be present in conjunction with a palmate membrane. When present together, the flanges form distal continuations of the membranes, giving the appearance of incomplete fusion of the membranes distally (pm, rf, fig. 12B). Flanges are usually best developed in the median and distal regions of the radioles.

Various outgrowths commonly referred to as stylodes, lappets, or external appendages may be present along the outer corners of the radioles. These structures may be poorly developed, as seen in *Pseudobranchiomma* Jones, represented only as low elevations (state 8b) or more well developed as seen in *Branchiomma* Kölliker (state 8c; st, fig. 13A). In the latter genus, stylodes are usually elon-

gate and filiform, clavate, or triangular. Stylodes are always paired, beginning near the base of the radioles and distributed to near the distal ends; spacing between each pair appears to be regular.

Photoreceptor cells or organs, in the form of simple ocelli, and simple or compound eyespots, are present on the radioles of some genera. Histological distinctions between these three forms in polychaetes were reviewed by Mill (1978). Simple ocelli are present in *Demonax microphthalmus* (Verrill, 1873; Perkins, 1984: simple eyespots). No consistent distribution has been reported at the generic level for simple ocelli. Simple eyespots (state 9b; se, fig. 13B) are found in *Notaulax* Tauber, *Hypsicomus* Grube, and *Anamobaea* Kröyer (Perkins, 1984: lensed ocelli). Simple eyespots are located along the lateral margins of the radioles, with distribution limited to an area just distal to the palmate membrane. Arrangement of eyes tends to be irregular along the radioles. Compound eyes (ce, fig. 13A), which have received greater attention systematically, may

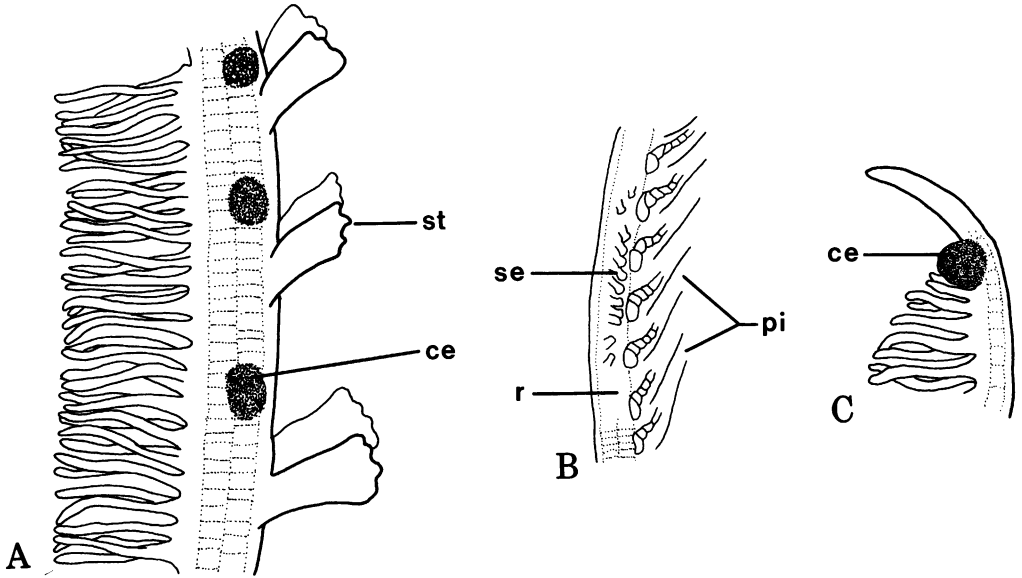


Fig. 13. A. Lateral view of radiole of *Branchiomma bombyx* (Dalyell) (after Rioja, 1923). B. Lateral view of radiole (median region) of *Notaulax rectangulata* Levinsen (after Perkins, 1984). C. Distal end (lateral view) of radiole of *Megalomma vesiculosum* (Montagu) (after Rioja, 1923).

be arranged as follows: (1) unpaired compound eyes, usually limited to proximal regions of radioles (state 9c; ce, fig. 15A), spacing between them is somewhat irregular, situated near the outer corners of the radioles; (2) a single compound eye per radiole, each limited to the distal end of one or more pairs of radioles (state 9d; ce, fig. 13C) just distal to the last pair of pinnules and situated along the inner margin of the radiole (but may also extend laterally to some extent); (3) paired compound eyes distributed along the length of the radioles (state 9e; ce, fig. 13A), each eye located on an outer corner of the radiole and regularly spaced.

On the inner margins of the branchial lobes may be dorsal and ventral extensions referred to as dorsal (= upper) and ventral (= lower) lips, respectively (dl, vl, fig. 14A, B). A number of histological and morphological studies have been conducted concerning this area of the branchial crown, especially in relation to structures associated with the dorsal lips (e.g., Claparède, 1873; Pruvot, 1885; Viallanes, 1886; Brunotti, 1888; Meyer, 1888; Johanson, 1927; Binard and Jeener, 1928; Nicol, 1931; Orrhage, 1980). As pointed out by Nicol (1931) and Orrhage (1980), a great deal

of confusion has existed as to interpretation of certain lip-associated structures and determination of homologies between the Sabellariidae, Sabellidae, and Serpulidae.

In the present study, many of the interpretations of structures, associated especially with the dorsal lips, follow from the work of Orrhage (1980). Consideration of this region in systematics has been very limited. Banse (1956, 1957) noted the presence or absence of dorsal and ventral lips in some of the fabriciini genera. Knight-Jones (1983) and Perkins (1984) recently placed greater emphasis on lip and lip-associated structures, apparently in response to Orrhage's (1980) observations.

The dorsal lips in sabellids extend from the inner, dorsal margins of the branchial lobes and terminate just dorsal to the mouth. They are usually erect and straight or may curve slightly at the same angle as the branchial lobes. The lips are ciliated, and, with the ventral lips (if present), may aid in sorting food particles collected by the radioles (Nicol, 1931; Lewis, 1968). In genera which lack radiolar appendages, the dorsal lips (state 10a) are usually low, rounded, slightly tapering structures, and tend to be somewhat thick-

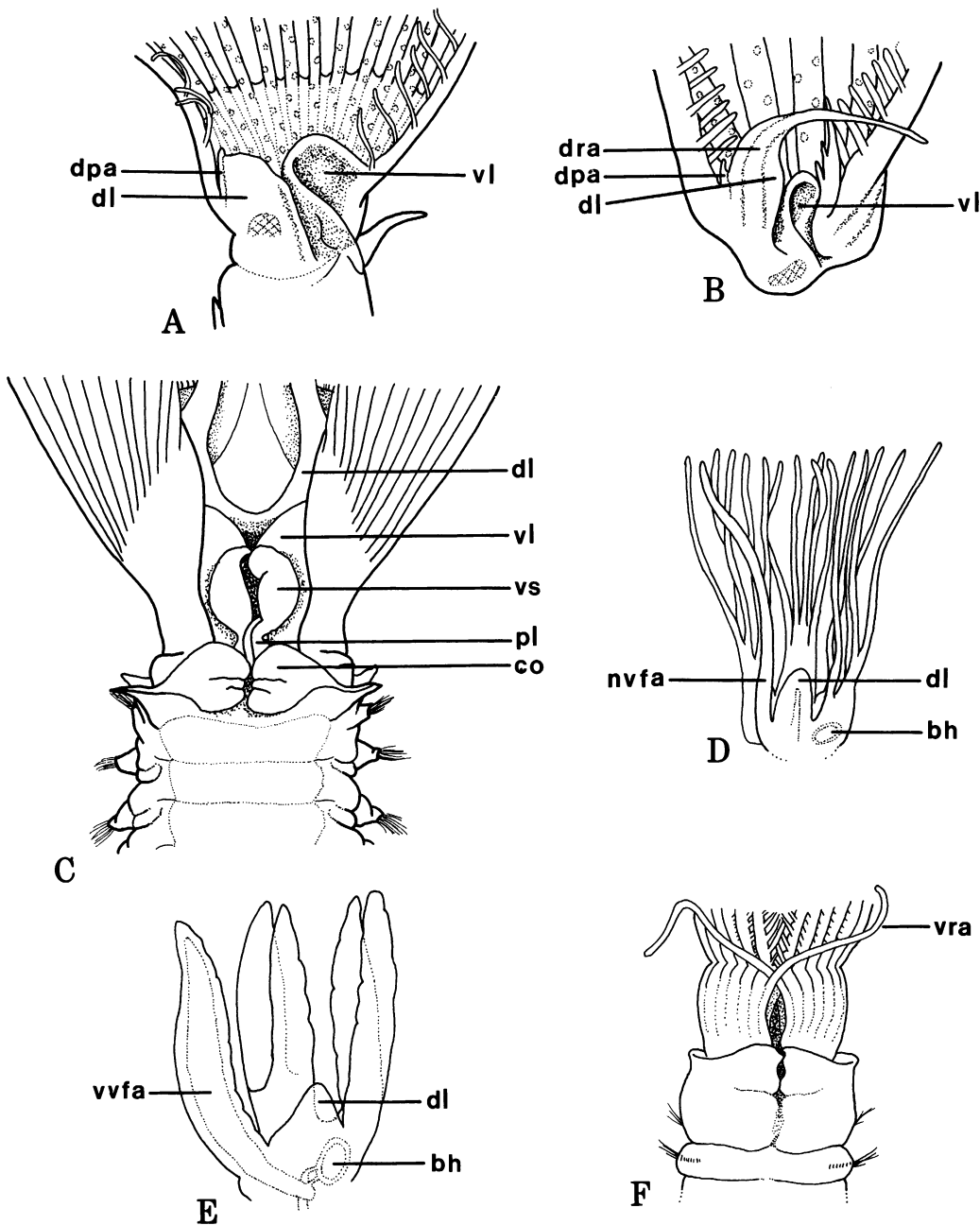


Fig. 14. A. Left half (inner view) of branchial crown of *Potamilla neglecta* (Sars). Cross-hatched area denotes transverse bar of branchial skeleton connecting lobes (after Knight-Jones, 1983). B. Left half (inner view) of branchial crown of *Demonax langerhansi* Knight-Jones (after Knight-Jones, 1983). C. Anterior end (ventral view) of *Sabella pavonina* Savigny (after Nicol, 1931). D. Right half (inner view) of branchial crown of *Fabriciella baltica* Friedrich (after Banse, 1956). E. Right half (inner view) of branchial crown of *Manayunkia aestivalis* (Bourne) (after Banse, 1956). F. Anterior end (ventral view) of *Jasmineira elegans* Saint-Joseph (after Day, 1967).

ened (dl, fig. 14A, D). Especially in small genera, the dorsal lips of this type suggest that they are inward-turned, ventrally directed extensions of the branchial lobes. This was illustrated by Lewis (1968: figs. 2, 3) for *Fabricia* and *Manayunkia*. Banse (1956, 1957) introduced schematic representations of the relations and occurrence of dorsal lips and other structures in this region.

Dorsal lips which contain radiolar appendages (sensu Perkins, 1984; state 10b) are usually more drawn out into elongate, triangular processes (dl, dra, fig. 14B). Orrhage (1980) found that the radiolar appendages are reduced radioles without pinnules which have migrated ventrally and fused medially with the dorsal lip. Dorsal lips with radiolar appendages are often somewhat thinner or more delicate than lips without these appendages. Perkins (1984) referred to dorsal lip regions dorsal and ventral to the radiolar appendages as upper and lower lamellae, respectively. Such secondary terms for these types of dorsal lips seem unnecessary and imply the derivation of new structures.

In some forms, the ventral edges of the dorsal lips may be fused with one another just dorsal to the mouth, forming what appears to be a transverse lamellar process. The systematic value of this structure at the generic level has not yet been determined. The degree of fusion may vary to such an extent that it is difficult to ascertain in small species. Dorsal lips may also be totally absent (state 10c); with no trace of any continuation of the branchial lobes.

In some genera, the dorsal margin of the dorsal lip extends up along the inner margin of the dorsalmost radiole and is fused with one or more of the more proximal pinnules (state 11b; Orrhage, 1980; Knight-Jones, 1983; Perkins, 1984). These pinnules are referred to as dorsal pinnular appendages (sensu Perkins, 1984) and may resemble more distal pinnules or may be somewhat shorter and thicker (dpa, fig. 14A, B). The number of dorsal pinnular appendages varies within a genus but their presence appears consistent. Knight-Jones (1983) and Perkins (1984) introduced the use of these structures as taxonomic characters.

The ventral lips (state 12a; vl, fig. 14A, B) extend from the ventral margin of the bran-

chial lobes; however, their orientation tends to be more variable than that seen in the dorsal lips. In very small genera, such as *Oriopsis*, or small species of *Chone* or *Euchone*, and in *Potamilla*, the ventral lips resemble the dorsal lips in being lobulate, slightly tapering structures (vl, fig. 12C). They extend dorsally to just below the dorsal lips and may only curve slightly along the inner margin of the branchial lobe.

In larger-bodied genera and species, the ventral lips extend dorsally from the ventral margin of the branchial lobe, more closely appressed to the inside of the lobe. Just below the dorsal lips the ventral lips turn toward the anterior midline then extend ventrally, terminating on either side of the mouth. The ventral lips are often the same height as dorsal lips minus the radiolar appendages. In larger-bodied species, the ventral lips tend to be rather thin and membranous, and the distal margin may appear plicate. Since the ventral lips tend to curve along the inner base of the branchial lobes and then turn ventrally, they are often wider than the dorsal lips.

In some species, the ventral lips may be partially fused ventral to the mouth (Nicol, 1931; Perkins, 1984). The absence of ventral lips (state 12b) has been noted in some genera, e.g., *Myxicola* (Meyer, 1888), *Fabriciola* (Banse, 1956), and *Augeneriella* (Banse, 1957).

In some genera the ventral lips may extend ventrally as lamellae along the anterior midline and terminate near or between the mid-ventral cleft of the collar (pl, fig. 14C). Perkins (1984) termed these structures parallel lamellae (state 13b; parallel folds sensu Nicol, 1931). He implied, however, that in instances in which parallel lamellae are present, the ventral lips "begin on the dorsal end" of these structures. Instead, as noted by Nicol (1931), the parallel lamellae are simply ventral continuations of the ventral lips. Just dorsal to the termination of the parallel lamellae there may be a pair of vesicles formed by the out-pocketing of the parallel lamellae. These vesicles were referred to as ventral sacs by Nicol (1931) and Perkins (1984); they are present in a number of species of various genera.

In the genera *Manayunkia*, *Fabriciola*, *Augeneriella*, and two undescribed genera, a pair of filamentous structures are situated just

ventral to the dorsal lips. These structures have been referred to as tentacles (Leidy, 1883; Lewis, 1968), palps (Annenkova, 1934; Friedrich, 1939; Hartman, 1951; Day, 1961, 1967), tentacular palps (Pettibone, 1953), ventral lips (Zenkevitch, 1925), or filaments (Banse, 1956, 1957). In the present study, the less ambiguous term, ventral filamentous appendages, is used, being derived from Banse's use of the term "filament." The systematic importance of this character was made obvious by Banse (1956, 1957), who recognized such appendages as representing an apomorphic condition (Banse, 1957).

The ventral filamentous appendages originate just ventral to the dorsal lips and are continuous with the ventral extensions of the dorsal inner margins of the branchial lobes (nvfa, vvfa, fig. 14D, E). The positional relationship of these appendages with other branchial crown structures was illustrated schematically by Banse (1956). The appendages are erect and usually extend to the distal end of the crown. Two types of appendages have been recognized as either nonvascularized (unbranched, state 14b) and vascularized (unbranched, state 14c; branched, state 14d). The nonvascularized form is slender, resembling a pinnule, but is slightly thicker; the external surface is relatively smooth (nvfa, fig. 14D). The vascularized form is considerably thicker, with a large blood vessel filling the interior (vvfa, fig. 14E). Communication of this vessel with the branchial hearts has been reported by Leidy (1883) and Banse (1956). In *Manayunkia* and two undescribed genera, these vascularized filaments are about the same thickness as the radioles. The surface of vascularized filaments tends to have numerous, minute wrinkles similar to those present on the pinnular surface in *Manayunkia* (discussed above, character 2).

A modification of the vascularized form is seen in *Augeneriella*, in which the filaments are branched. The general dimensions of these filaments are unchanged except that there is a proximal stem from which arises two to seven branches. The relative number and pattern of branches, and ontogeny of branching, appears to be species specific (personal obs.).

The terms "vascularized" and "nonvascularized" may not be appropriate. The non-

vascularized condition might actually contain a narrow blood vessel. As with pinnules, the narrowness of this structure makes it difficult to determine, based only on general observation, if a vessel is present or not. Detailed histological studies have not been conducted for either the nonvascularized or vascularized ventral filaments. Zenkevitch (1925) did illustrate a series of transverse sections through *Manayunkia baicalensis* but gave no details of the ventral filamentous appendages.

Possible homologies between the ventral filamentous appendages and other branchial crown structures are unknown. This structure may be homologous to the radiolar appendages, representing a reduced and displaced radiole, or a modified proximal pinnule of the dorsalmost radiole. At this time, the nonvascularized and vascularized forms are considered homologous because of unique positional similarities. Ciliation of these structures has only been reported sporadically (e.g., Leidy, 1883; Zenkevitch, 1925).

Just lateral to the ventralmost radioles and emerging from the ventral anterior margin of the branchial lobes may be a series of filamentous structures referred to here as ventral radiolar appendages (state 15b; vra, figs. 12B, C, 14F). The ventral radiolar appendages, varying in number from one to about five, are thickened, smooth filaments which may be as long as the radioles but are more commonly only about one-half to one-quarter the radiole length. The appendages are not quite as thick as the radioles but are thicker than the pinnules. Various authors have referred to these structures as filaments (Banse, 1956, 1957), ventral filaments (Day, 1967; Knight-Jones, 1983), naked ventral filaments (Banse, 1972), or radioles without pinnules (Hobson and Banse, 1981).

Taxonomic recognition of the ventral radiolar appendages has been limited (e.g., Rioja, 1923, for *Jasmineira elegans* Saint-Joseph; Banse, 1957, for *Oriopsis*) probably because of ambiguities with regard to homology and terminology. Banse (1957) used the term "filaments" with reference to both the ventral filamentous appendages of *Augeneriella* and ventral radiolar appendages in *Oriopsis*. Although he indicated positional differences for both types of structures, there

did not appear to be any explicit or implicit differences noted in terms of homology.

Banse did mention that in *Chone infundibuliformis* Kröyer, structures similar to those seen in *Oriopsis* occur in an analogous region on the dorsal side of the branchial lobes. These latter structures possess a branchial skeleton similar to that of pinnules but he could not discern a skeleton in such structures occurring ventrally. Skeletal similarities notwithstanding, Banse suggested that these dorsal structures are "selbständig" (independent) of the dorsalmost radiole, thereby implying that the dorsal structures represent reduced radioles. Yet Banse did not extend this consideration to the ventral radiolar appendages of any genus, nor did he cite Rioja (1923), who suggested that the ventral filaments of *Jasmineira elegans* might be degenerate radioles.

Day (1961) continued the problem by criticizing Banse's work on *Oriopsis* for having "laid too great a stress on the filamentous structures(?palps). . . ." Day considered it difficult at times to distinguish these ventral structures as "palps" or basal pinnules. He subsequently (1967) called the ventral radiolar appendages of *Oriopsis* "ventral filaments," whereas the corresponding ventral structures in *Chone*, *Euchone*, and *Jasmineira* were considered ventral radioles which lack pinnules.

Later workers (e.g., Hobson and Banse, 1981; Knight-Jones, 1983) have viewed these structures as radioles without pinnules in *Oriopsis*. Hartman (1944) referred to dorsal radiolar appendages in *Chone minuta* Hartman, which were not attached to the dorsal lip, as "filamentous radioles" (see below).

Examination of various genera (including *Oriopsis*) for the present study supports views that these structures are reduced radioles. In large specimens of *Chone* the ventral radiolar appendages are connected by a palmar membrane to well-developed radioles. In some instances, these appendages do have reduced pinnules proximally. Contrary to Banse's (1957) observations, a skeleton is present in the ventral radiolar appendages of *C. infundibuliformis*. The axial skeleton of the ventral radiolar appendages is in most genera only one cell wide, but in some species of *Jasmineira* two rows of cells have been observed.

The question of this radiolar appendage being a pinnule in *Oriopsis* does not appear to hold; if the axial skeleton is traced from the appendages, it can be shown to originate directly from the U-shaped axial skeleton of the branchial lobes. Thus, the ventral radiolar appendage is considered homologous in all genera possessing such a structure, being the remnants of incompletely formed ventral radioles.

The term "ventral radiolar appendage" is applied here to indicate similarities to the dorsal radiolar appendage, i.e., both are reduced radioles occurring at the extreme ends of ventral and dorsal radiolar distributions. The fact that the dorsal radiolar appendages were recognized by Orrhage (1980), Knight-Jones (1983), and Perkins (1984) only as structures fused with the dorsal lips does not limit recognition of similarly reduced dorsal structures which are not fused with the dorsal lips. These two conditions can, if necessary, be denoted as separate states of the same character. The presence of dorsal radiolar appendages not fused to the dorsal lips was not considered in the present study since this state does not appear to be generically consistent.

The dorsolateral margins of the branchial lobes are rounded in genera in which the lobes are separate (state 16a; bl, fig. 10). In most genera with fused lobes, the transverse area of fusion is slightly recessed and the dorso-lateral margins of the lobes can be seen as a pair of rounded shelves (state 16a). In several genera, the lateral margins of these shelves are drawn out as thin flanges (state 16b; dbbf, figs. 15A, 18B) which have been used taxonomically by various workers (e.g., Bush, 1905; Hartman, 1938; Knight-Jones, 1983; Perkins, 1984). Bush (1905) appears to have implied sister-group relationships among *Pseudopotamilla*, *Eudistylia*, and *Schizobranchia* based in part on the presence of these flanges.

In *Anamobaea* Kröyer and *Amphiglena* Claparède there are a pair of thin, erect, membranous flanges, referred to here as ventral basal flanges (state 17b; vbf, fig. 15B), which extend anteriorly from the ventral side of the peristomium to the outer ventral margins of the branchial lobes. These flanges are best developed in *Anamobaea*, in which an analogous dorsal pair is also present (fig. 15B). No histological studies have been conducted

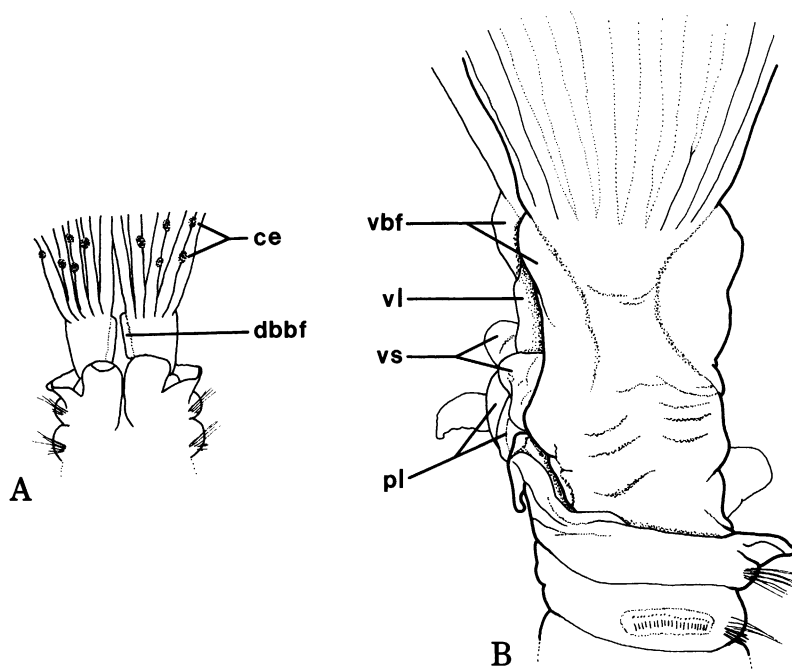


Fig. 15. A. Anterior end (dorsal view) of *Pseudopotamilla reniformis* (Bruguiera) (after Knight-Jones, 1983). B. Anterior end (lateral view, left side) of *Anamobaea orstedii* Kröyer (FSBC I 33810).

to determine if the ventral structures are actually homologous in the two genera.

NONSETAL CHARACTERS OF THE THORAX AND ABDOMEN

Developmental studies of the Sabellidae and Serpulidae (e.g., Wilson, 1936; Segrove, 1941, respectively) have indicated that the peristomium is the region anterior to setiger 1 and posterior to the branchial crown. The branchial crown originates as paired, dorsal outgrowths of the prostomium. During metamorphosis the remainder of the prostomium apparently becomes completely reduced such that the branchial crown is the only remnant of this region and with the brain present in the peristomium. Schroeder and Hermans (1975) reviewed the development of views on the demarcation of prostomium, peristomium, and body segments. For the present study, the definitions of prostomium and peristomium given by Schroeder and Hermans (1975: 159) are used: "The prostomium is that region of the annelid body originating anterior to the prototroch or the primary trochoblasts. . . . The peristomium is that region containing the mouth opening,

originating in front of the most anterior segment and including the prototroch and metatroch."

In many small-bodied sabellid genera, e.g., *Manayunkia*, *Fabricia*, and *Oriopsis*, close examination of the region between the branchial crown and the anterior margin of setiger 1 reveals that two rings are present in what is here regarded as peristomial in nature (cs, bs, fig. 16D). It must be stressed that the term "rings" in this instance is strictly descriptive; the entire area will be regarded at this time as peristomial. The anterior part of the peristomium is here called the anterior peristomial ring and is the area of attachment for the branchial crown and bears the mouth. The posterior part of the peristomium is referred to as the posterior peristomial ring.

Demarcation of these peristomial regions is variable; in some of the species in most small-bodied genera examined, the annulation is distinct ventrally and laterally (see e.g., Fitzhugh, 1983). Width of the two rings is variable except in genera with large-bodied species, where the anterior ring is narrower. Concomitant with this trend is a tendency toward loss of the annulation, possibly due

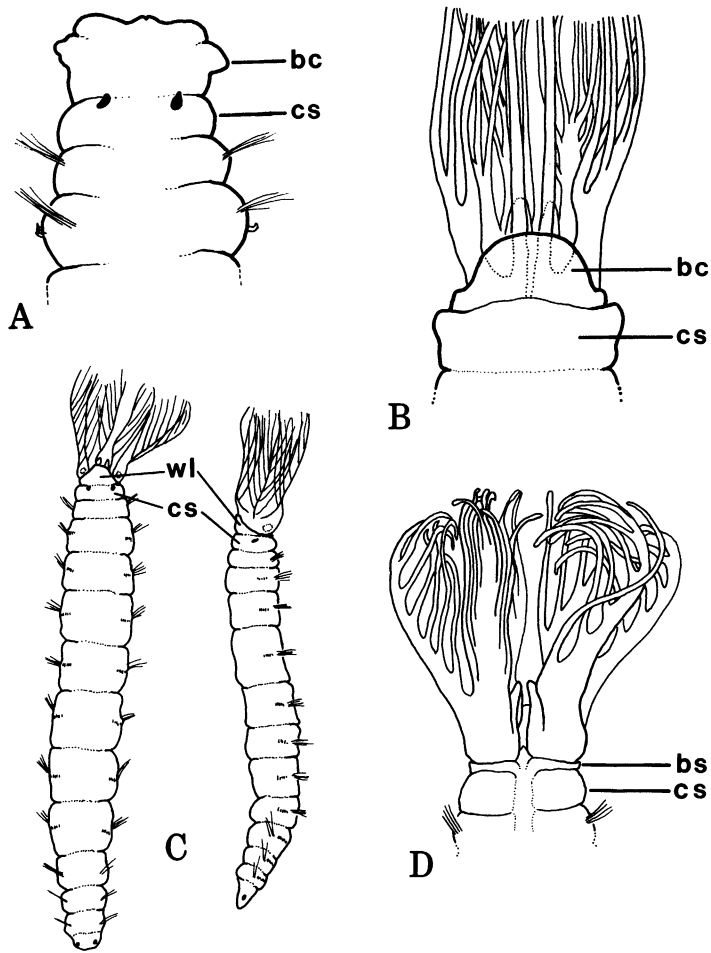


Fig. 16. A. Anterior end (dorsal view) of *Fabriciolo australiensis* Hartmann-Schröder, branchial crown removed (after Hartmann-Schröder, 1981). B. Anterior end (ventral view) of *Fabriciolo baltica* Friedrich (after Banse, 1956). C. *Fabricia sabella* (Ehrenberg), ventral view (left) and lateral view of the left side (right; after Banse, 1956). D. Anterior end (dorsal view) of *Fabricia sabella* (after Banse, 1956).

to the anterior extension of the posterior ring over the anterior ring, or extensive fusion of the two areas such that the distinct nature of these regions becomes obscure. This latter situation appears to occur in the Serpulidae, making it difficult to determine if a two-ringed peristomium is also present in that family. For purposes of the present study, similarities in the peristomium of the serpulids with large-bodied sabellid genera are considered homologous.

Recognition of these two peristomial rings is necessary to denote the apparent nonhomologous condition between various structures which have been traditionally referred

to as the "collar." The plesiomorphic condition for the anterior peristomial ring is that of a low, even segment (state 18a). From this state can be derived several apomorphic conditions in which the anterior margin of the anterior peristomial ring might be modified into some form of anterior projection, herein called an anterior peristomial ring collar or lobe.

These anterior peristomial ring outgrowths may be in the form of a membrane or lobe. In the membranous condition (state 18b; e.g., *Manayunkia* and *Fabriciolo*; bc, fig. 16A, B) the anterior peristomial ring collar is usually separated by a narrow gap middorsally but

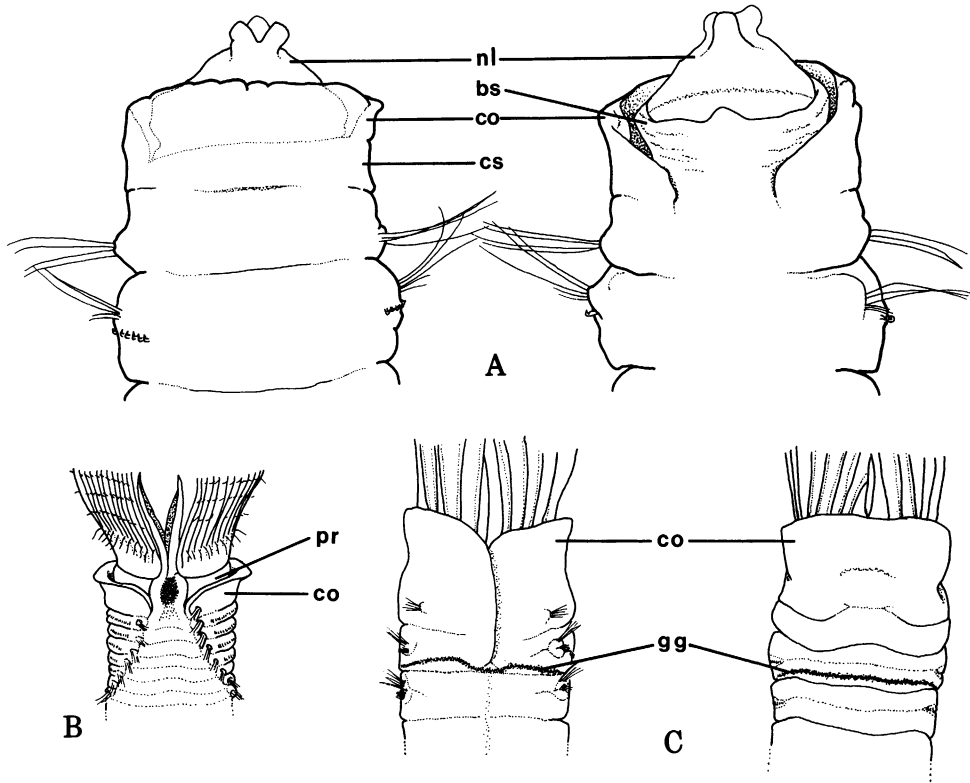


Fig. 17. A. Anterior end of *Oriopsis armandi* Claparède (MNHP 264), branchial crown removed, dorsal (right) and ventral (left) views. B. Anterior end (dorsal view) of *Branchiomma nigromaculata* (Baird) (after Day, 1967). C. Anterior end of *Chone infundibuliformis* Kröyer (after Hartmann-Schröder, 1971), dorsal (left) and ventral (right) views.

otherwise is of the same height all around or slightly higher ventrally. Alternatively, the anterior extension of the anterior peristomial ring may be limited to a wide ventral lobe (state 18c; wl, fig. 16C) or a narrow ventral lobe (state 18d; nl, fig. 17A). The wide lobe is a thick, rounded, conical structure (e.g., *Fabricia*, *Augeneriella*). Of the genera examined, this lobe is somewhat longer than the membranous anterior peristomial ring collar. The narrow ventral lobe is common in most sabellid genera. It is in the same position as the wide lobe but is distinctly narrower, usually triangular in shape, and comparatively shorter. In many fabriciini genera the narrow lobe is distally bifid or trifid; the degree to which this is generically consistent has not yet been determined. In most large-bodied genera, particularly the Sabellinae, a reduction of the anterior peristomial ring is accompanied by size reduction of the narrow

lobe, with the lobe becoming hidden by the ventral lips or parallel lamellae.

In the taxonomic literature, the membranous or wide-lobe conditions of the anterior peristomial ring have been viewed as homologous with what has been considered the traditional type of collar seen in most other sabellids and apparently all serpulids.

The narrow lobe condition has not received much attention although Banse (1957) did refer to it in his diagnosis of *Oriopsis* and has illustrated it at times (Banse, 1957, 1970). He (1957) stated, however, that the distal end of the narrow lobe carries the mouth in *Oriopsis*. Examination of *O. armandi* (Claparède) and *O. hynensis* Knight-Jones indicates that the mouth is located dorsal to the lobe as it is in other sabellids. Day (1961) apparently confused the narrow lobe of *Oriopsis* with the ventral lips.

What is more commonly recognized as the

collar (state 19a; co, fig. 17A–C) in serpulids and sabellids is actually a membranous outgrowth originating from the posterior margin of the posterior peristomial ring. Because of the apparent confusion between anterior and posterior peristomial ring collars, workers have incorrectly referred to the peristomium as being a single, collar-bearing segment. The posterior peristomial ring collar is always interrupted by a gap middorsally and may otherwise be entire or divided into several “collar lobes.” The margin(s) of this collar may be incised or notched to varying degrees. Bush (1905) attempted to establish collar structure as a generic-level taxonomic character. Her views have apparently not been followed, probably as a result of Johansson’s (1927) statement that collar conditions are not generically consistent (see also statements by Banse, 1972).

Bush remarked that it might be possible to arrange collar forms into an evolutionary transformation series for the Sabellidae (assuming homology of all “collar” types, which is not the case). The absence of the collar would be the primitive condition. The initial derived state might be a collar which is entire or divided into two lobes, a more derived state then being developed with four lobes. Bush did not consider the serpulid collar in determining polarity of sabellid collar states.

In the present study, only the presence or absence of a collar has been used. The degree of variability in collar construction has not been accessed thoroughly enough to allow inclusion in the present study. T. H. Perkins (personal commun.) suggests, however, that there is generally strong consistency in posterior peristomial-ring collar form at the generic level (but see below).

As mentioned above, the states manifesting the anterior peristomial ring outgrowths (states 18b–d) are not homologous with the posterior peristomial ring collar (state 19a); the narrow lobe state (18d) is commonly present in conjunction with the latter structure (co, nl, cf. fig. 17A). If the membranous collar and wide-lobe state of the anterior peristomial ring are considered homologous to the narrow-lobe state, then fabriciins such as *Fabricia*, *Manayunkia*, *Augeneriella*, and *Desdemonia* are characterized as lacking the more common posterior peristomial ring collar seen in most sabellids and serpulids. Note that the

membranous collar state of the anterior peristomial ring is never present at the same time as either lobed state in this latter group; this is the predicted condition if the two structures are homologous (Patterson, 1982).

Epidermal glandular regions in serpulids and sabellids are extensive and may be diffuse or limited as ventral glandular shields. In addition, some genera have what has been referred to as a postsetal glandular girdle or ridge (state 20b; fig. 17C, gg). The glandular girdle is a complete or incomplete whitish band which is limited to about the posterior quarter of setiger 2, just posterior to the neuropodial uncini. When incomplete around the segment, the girdle is usually best developed ventrally and laterally. In the specimens examined, no distinct gland cells could be discerned, the girdle being comprised of slightly opaque material which is not partitioned into what would appear to be cells. The anterior and posterior borders of the girdle are smooth or may appear vesiculate. The glandular nature of the girdle is yet to be confirmed since no histological studies have been published. The term glandular girdle is retained here simply for the sake of terminological consistency.

Following Hofsommer (1913), Banse (1970) applied methyl green staining to epidermal mucous cells in *Euchone*. The procedure was continued by Banse (1972, 1979), Fitzhugh (1983), and Uebelacker (1984a). The glandular girdle has not been shown to take up the stain (e.g., Banse, 1970, 1982; Uebelacker, 1984a). Thus, either the girdle is not a glandular epidermal structure, or it may be glandular and subepidermal, or a glandular structure which does not accept methyl green.

Although illustrated sporadically (e.g., Fauvel, 1927; Day, 1967), use of the glandular girdle as a systematic character was not begun until later by Banse (1970) for *Euchone*. Banse (1972) then included this character in his diagnosis of *Chone* and noted that glandular girdles are also present in *Jasmineira* and *Myxicola*. Knight-Jones (1983) included the character in the diagnosis of *Potamethus* Chamberlin and Hartmann-Schröder (1986) noted a thin glandular girdle on the new species *Oriopsis cincta*; this structure has also been observed on other species of *Oriopsis* (personal obs.).

Banse (1972) considered presence of the

glandular girdle to be a primitive feature, based in part on his assumption that *Chone* and *Euchone* are primitive genera (fig. 9; see Banse, 1957, 1970) and because similar girdles are seen in other families such as the Terebellidae. In the present study, consistent with the use of the Serpulidae as an outgroup, the glandular girdle cannot necessarily be considered primitive at this time. If, however, the ventral glandular "building organ" of setiger 2 of sabellariids can be shown to be homologous to the sabellid glandular girdle, then such a structure could be considered primitive and its loss (reversal) apomorphic in the Serpulidae.

Ocular units in the thorax and abdomen of some genera appear to be organized as simple eyespots. These are referred to as interrampal eyes (state 21b; se, fig. 20D, E) in that they occur between the notopodial and neuropodial tori. cursory examination of a single eye appears to indicate a spherical lens on top of an elongate, conical pigmented region. The pigmented region appears to surround a translucent area presumed to be the location of a receptor cell. The eye is positioned perpendicular to the body surface. The epithelium over the eye may be pigmented in a circular pattern slightly larger than the eye itself (fig. 20E).

Interrampal eyes have never been used for systematic purposes, even though they appear to be consistently present within some genera. The eyes (or overlying pigment) have been illustrated in various works but not referred to directly (e.g., Nicol, 1931; Day, 1967). In other instances, only the superficial pigment spots have been mentioned and/or illustrated (e.g., Claparède, 1873; McIntosh, 1923; Rioja, 1929; Jones, 1962; Hartmann-Schröder, 1971; Uebelacker, 1984a). Berrill (1977a) illustrated the interrampal eyes of *Branchiomma nigromaculata* (Baird), identifying them as ocelli. His illustrations appear to differentiate between the overlying pigment spot and the eye itself. Meyer (1888) noted that interrampal pigment spots and structures resembling the ocelli found in the brain are present in a number of sabellid taxa, including *Spirographis* (= *Sabella*).

The notosetae of setiger 1, commonly referred to as collar setae, may be grouped as two different fascicle types. In the plesiomorphic condition (i.e., present in the Ser-

pulidae and most sabellid genera), the fascicle resembles a slightly oblique bundle (state 22a; fig. 18A), comprising a superior and inferior row(s). Setae of both rows usually resemble the superior notosetae of other thoracic setigers (discussed below) except that the inferior setae are usually shorter than those of the superior row. The superior row may form a slight arc above the oblique inferior row(s) or they may be obliquely parallel. In the apomorphic condition, the fascicle is in the form of a single, slightly oblique to longitudinal, elongate row of setae (state 22b; setf, fig. 18).

Thoracic notosetal fascicles beginning with setiger 2 can also be identified as having superior and inferior setal groups. The superior notosetae form an arc over the inferior notosetae (sup, e.g., fig. 19B). The curvature and placement of this arc is variable, resulting in it sometimes being displaced almost as an anterodorsal or posterodorsal arc relative to the inferior setae, or situated squarely above the inferior setae. The inferior notosetae may be organized into one to usually no more than three roughly parallel rows, oriented transverse or slightly oblique to the longitudinal body axis (state 23a; pal, fig. 19A–C). This transverse or oblique arrangement may be modified such that the setae are grouped as a circular or ovoid bundle with roughly longitudinal rows (state 23b; spine, fig. 19D).

In *Myxicola*, the notosetae are distributed irregularly within a circular fascicle such that no pattern of orientation can be discerned (state 23c; noto, fig. 19E). A problem with this genus is that the thoracic notosetae do not appear differentiated into superior and inferior groups. At this time, these fascicles are considered homologous to the superior notosetae. Whether the inferior notosetae have been lost or are grouped with the superior notosetae is not yet known.

Abdominal neuropodial tori may be separated into one of three states. The most common form occurs in serpulids and most sabellids, in which it is a roughly transverse ridge or swelling (state 24a; neurop, fig. 20B, C). Each torus may become shortened and drawn out as an erect, conical lobe (state 24b; fig. 20A), or reduced to a low, circular elevation or swelling as seen in *Myxicola* (state 24c; fig. 19E). Associated with the shape of the tori, the abdominal neurosetal fascicles may be of several kinds. The transverse ridge

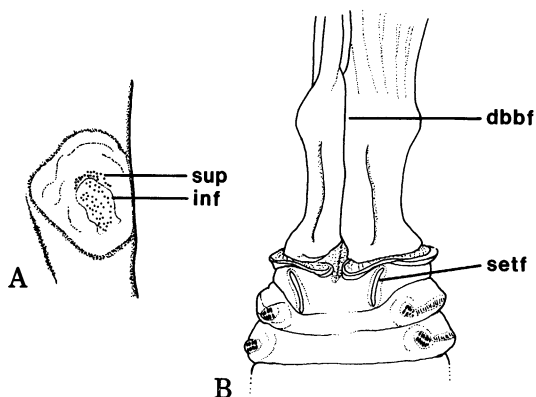


Fig. 18. A. Distribution (slightly schematic) of superior and inferior setae of setiger 1 (left side) of *Eudistylia vancouveri* Bush (USNM 44862) as emerging from the body. B. Anterior end (dorsal view) of *Notaulax nudicollis* (Kröyer) (after Perkins, 1984).

form may have transverse fascicles (state 25a) of one or more rows of setae. Generally, these rows can be roughly differentiated into anterior and posterior groups, each comprising 1–2 rows each (neuop, fig. 20B, C).

Conical tori may have fascicles oriented in two rows, in which what is here interpreted to be the anterior row is curved into a C-shape, with a bundle of setae in the middle of the C, representing the posterior row (state 25b; fig. 20D, E). In another type of fascicle associated with conical tori, the posterior setal row is apparently lost and the anterior row has been arranged into a tight spiral pattern (state 25c; fig. 20F).

In *Myxicola*, the low, rounded tori possess an irregular bundle of setae, resembling the pattern seen in thoracic notopodia (state 25d; fig. 19E). As with thoracic notosetae, it is not known if the abdominal neurosetae represent only the anterior or posterior rows, or fusion of the two. At this time, the bundle is assumed to be derived from the anterior row.

The interpretation of anterior and posterior setal rows for states 25b–d was determined from general considerations of transformation series of setal forms in the transverse rows in the outgroup and ingroup genera. This is explained below for the abdominal neurosetal forms.

On the posterolateral region of the pygidium of some fabriciina genera are a pair of

black, circular eyespots (state 26b; pe, fig. 21). These structures may be simple ocelli since no differentiation of a lens or sensory cell has been seen. Pygidial eyespots are consistently present within the *Fabricia-Fabriciolo-Augeneriella* complex and have been used by numerous workers for recognizing this grouping. Pygidial eyespots have also been reported in *Oriopsis*, *Myxicola*, and various genera of Sabellinae. Meyer (1888) considered pygidial eyes to be primitive since they reportedly occur in other polychaete families and because of the hypothesized free-living nature of the serpulacean ancestor. However, no consistency of occurrence has been noted in these other polychaete families nor has the homology of these eyes been demonstrated. For this study, pygidial eyespots were not recognized in these latter groups since they were not observed in the type species.

THORACIC NOTOSETAL CHARACTERS

The thoracic notosetae of the Sabellidae have been recognized as taxonomically important for quite some time although distinctions between types have been limited and not consistently applied. The setal types and terminology described below have been adopted in part from Perkins (1984), such that thoracic notosetal and abdominal neurosetal forms are placed within respective transformation series on the basis of setal shaft and hood construction, and orientation. A similar view was presented by Knight-Jones (1983).

Perkins (1984) further suggested differentiating between “setae” and “uncini,” the distinction being that “setae” occur only in thoracic notopodia and abdominal neuropodia, and vice versa for “uncini.” Such an interpretation of the term “seta” will not be used here for it potentially implies nonhomology between notosetal and neurosetal structures. The definition of seta given by Fauchald (1977: 160) does denote this homology: “secretion from the parapodia forming the armature of these structures.” Thus, the term “uncini” is used to denote a subset of structures grouped within the more inclusive term “setae.”

Ultrastructurally, all forms of annelid setae are similar. A general review of annelid setal

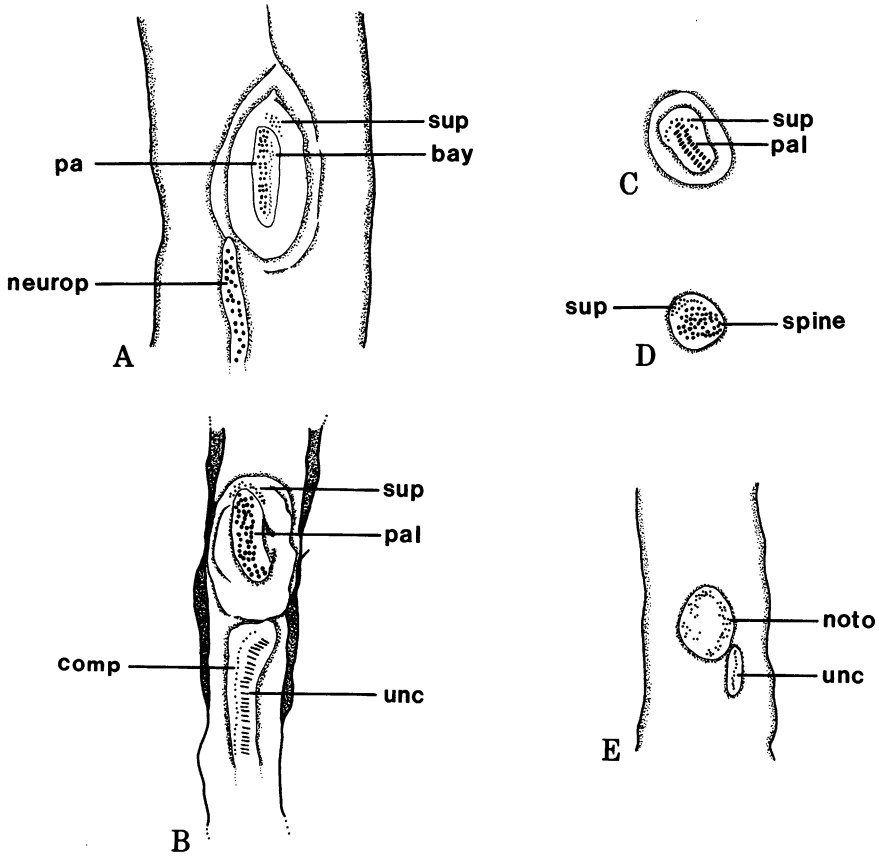


Fig. 19. Distribution of thoracic setal forms. A. Setiger 4, lateral view, right side, from *Chone infundibuliformis* Kröyer (USNM 41517). B. Setiger 5, lateral view, left side, from *Schizobranchia insignis* Bush (USNM 40333). C. Distribution (schematic) of superior and inferior setae of setiger 2 (left side), from *Notaulax occidentalis* (Baird) (USNM 16245). D. Distribution (schematic) of superior and inferior setae of setiger 6 (left side), from *Sabella pavonina* Savigny (USNM 19618). E. Lateral view (schematic) of setiger 3 (left side), from *Myxicola infundibulum* (Renier) (USNM 44813).

structure is given by Richards (1978) and more specific treatments are provided, for example, by Bouligand (1966, 1967), Orhage (1971), Gustus and Cloney (1972), and George and Southward (1973). A seta is composed of a series of longitudinal canals which may be partitioned by transverse septa, with a fibrillar, chitin-protein material deposited between the canals (Richards, 1978). Discussion of tissue components operating in setal formation are presented by Bouligand (1967) and Richards (1978). The size and distribution of longitudinal canals and distribution of fibrillar material partly determine the shape and appearance of a seta. Commonly, a seta has an inner medulla and outer cortex. The cortex usually contains canals of

widest diameter but these decrease in size toward the periphery, with the medulla containing the narrowest canals and greatest amount of fibrillar material (but see below). Sabellid thoracic notosetal and abdominal neurosetal types are very uniform with respect to general construction. The emergent part of the seta is composed of a shaft with tightly packed, narrow canals, which is surrounded distally or subdistally, at least in part, by a hoodlike structure (see figs. 22A–F, 23A–C, 24C–F). This “hood” is composed of a thin layer of loosely packed microtubules which are continuations of the shaft canals (e.g., Knight-Jones, 1981). The orientation of these microtubules probably determines the striation patterns seen on the hood in light

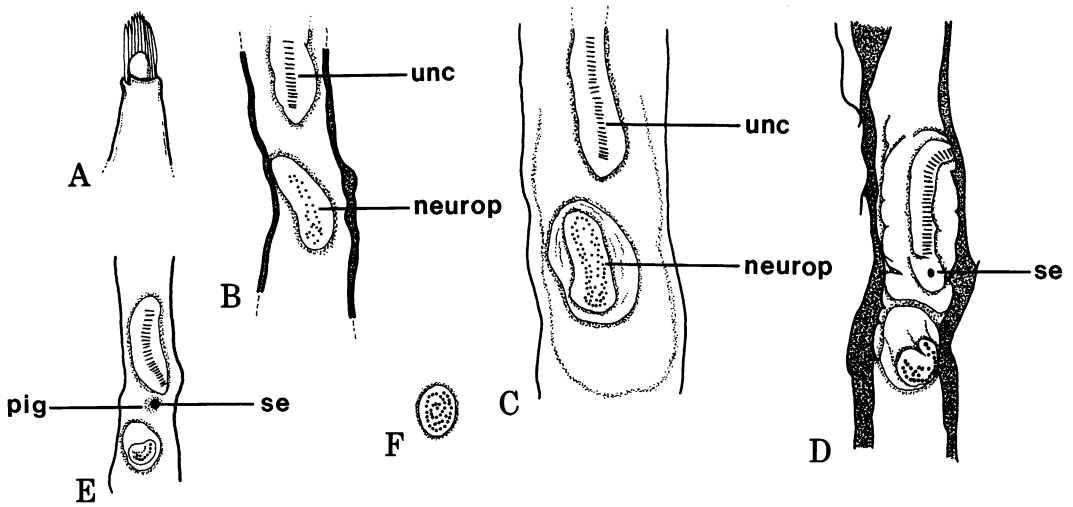


Fig. 20. Distribution of abdominal setal forms. A. Neuropodium (dorsal view) of setiger 12, from *Bispira voluticornis* (Montagu) (FSBC I 32292). B. Lateral view of setiger 15 (right side), from *Schizobranchia insignis* Bush (USNM 40333). C. Lateral view of setiger 14 (left side) from *Eudistylia vancouveri* (Kinberg) (USNM 44862). D. Lateral view of setiger 13 (left side) from *Bispira voluticornis* (FSBC I 32292). E. Lateral view of setiger 24 (left side) from *Branchiomma nigromaculata* (Baird) (USNM 43507). F. Distribution (schematic) of setiger 24 neurosetae from *Sabella pavonina* Savigny (USNM 19618).

microscopy. The distal ends of microtubules may become separated from one another, giving the surface of the hood a slightly serrated or ragged appearance. Between the hood and shaft are a series of irregular lacunar spaces (Perkins, 1984). The shaft may terminate within the hood or extend to the end of the seta. Based on the micrographs of Perkins (1984), demarcation of a medulla and

cortex is not apparent in the hooded region. It may be possible that the hood is a distal continuation of the cortex, separated from the medullar shaft.

Previous taxonomic accounts of sabellid setae have usually identified the hood as a "limbation" or "wing" of the shaft with the "spatulate" condition being a modification of this form. In very small setae there may only be a loose association of microtubules along one margin of the shaft without the formation of lacunae. In light microscopy, this would appear similar to a hood but might actually be more appropriately viewed as a limbation. Further work of the type presented by Perkins (1984) is needed to understand better the placement of microtubules and classification of setal types.

Six thoracic notosetal forms are described in the present study and then their distributions as stated in characters 27–31 are discussed.

Elongate, narrowly hooded setae (sensu Perkins, 1984; fig. 22A, B) have been most commonly referred to as limbate. According to Perkins (1984), the shaft is roughly circular in cross section. A narrow hood begins distally and extends with the shaft to near the

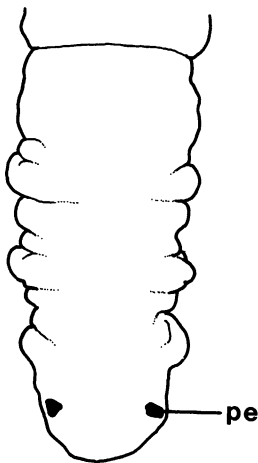


Fig. 21. Posterior end (dorsal view) of *Fabricia infratorquata* Fitzhugh (after Fitzhugh, 1983).

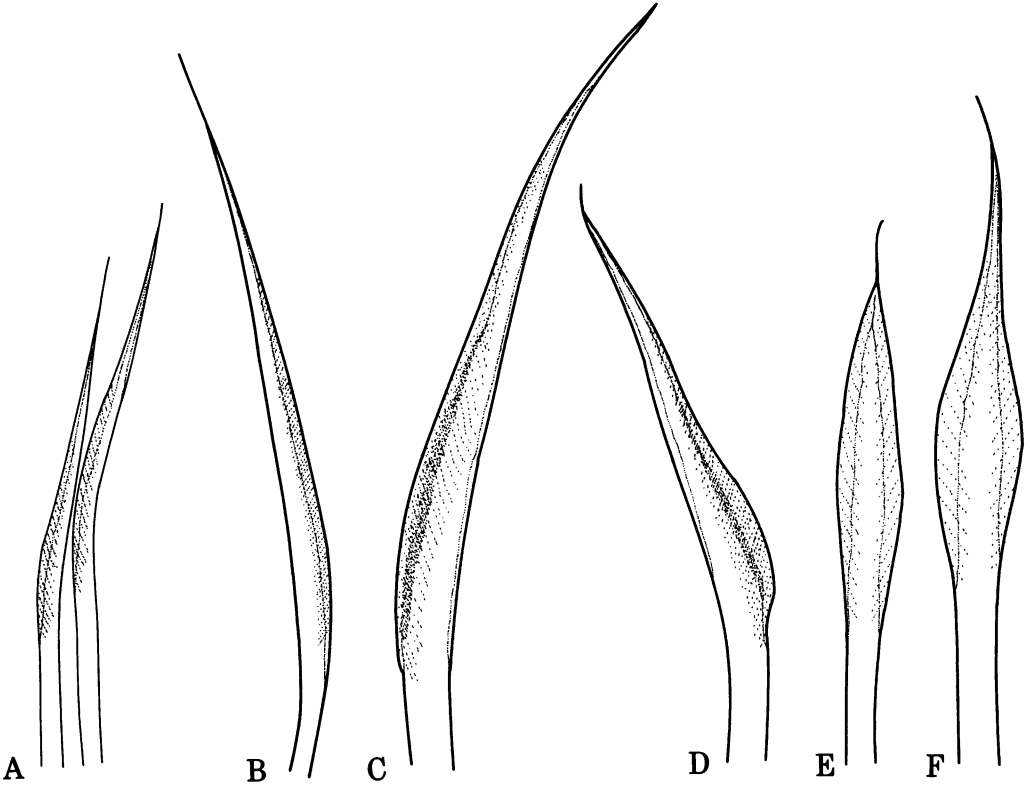


Fig. 22. Elongate, narrowly hooded setae: **A**, from superior notopodial arc, setiger 3, *Schizobranchia insignis* Bush (USNM 40333); **B**, from posterior neuropodial row, setiger 30, *Megalomma* sp. A (USNM 53976). Spinelike setae: **C**, **D**, long and short forms from inferior notopodial group, setiger 4, *Sabella pavonina* Savigny (USNM 19618). Broadly hooded setae: **E**, **F**, short and long forms from inferior notopodial rows, setiger 8, *Megalomma* sp. A (USNM 53976).

tip of the seta. The shaft is bent at a slight angle at the proximal origin of the hood, with the hood situated on the convex side. The hood is widest proximally, becoming narrower distally. The lacunar spaces are widest on the convex side of the shaft, extending around the shaft and terminating laterally. Both superior and inferior notosetae are elongate and narrowly hooded in the Serpulidae examined. Rioja (1929) considered this (i.e., "limbate setae") to be a primitive setal form from which other thoracic notosetal forms are derived.

Spinelike setae (or spine-like sensu Perkins, 1984; fig. 22C, D) are similar to elongate, narrowly hooded setae in general outline and appear to be narrowly hooded. But they tend not to display the narrower, more slender appearance of elongate, narrowly hooded setae and are thus stouter. The hood of spinelike

setae usually displays more distinct surface striations which result in the hood being less translucent. In cross section, the shaft is more compressed laterally than in elongate, narrowly hooded setae, but the hood is similar in both forms (Perkins, 1984). Lacunar spaces are widest on the convex side of the shaft, terminating laterally. The distinct appearance of spinelike setae has been noticed by various workers who have referred to them as "cimitarra" setae (e.g., Rioja, 1923) or "knife-blade" setae (e.g., McIntosh, 1922, 1923).

Broadly hooded setae (sensu Perkins, 1984; fig. 22E, F), commonly referred to as "subspatulate" setae, are slender forms generally appearing intermediate between narrowly hooded and paleate setae. The emergent part of the shaft is straight, with a short, distal hood. The hooded area of the shaft may be

straight or very gently curved. In profile the median region of the hood is widest, gently tapering distally to a fine, sometimes elongate tip. The shaft does not seem to continue into the distalmost region of the hood. The hood and lacunae appear to surround the shaft completely, but Perkins' (1984) micrograph of a cross section indicates that the hood and lacunae are arranged similarly to those seen in narrowly hooded and spinelike setae. The shaft in the hooded region is oval in cross section with the longest axis being perpendicular to the long axis of the hood. A problem in defining broadly hooded setae is that there may be a range of hood widths verging on the narrowly hooded or paleate condition (see Perkins, 1984). Additional work will be necessary to determine if the broadly hooded state can be regarded as a distinct form or part of a continuum of several setal types.

Paleate setae (*sensu* Perkins, 1984; fig. 23A–C), which have also been referred to as “spatulate” setae, are very stout, hooded setae. The straight, emergent shaft is thick and is usually short. The hooded region of the shaft is relatively straight or slightly curved, and does not appear to continue to the distal end of the hood. The hood is short, extending from the shaft abruptly and is widest medially or near the distal end. The distal end of the hood narrows abruptly and may terminate as a broadly rounded end (fig. 23C) or may be surmounted by a mucronate tip (fig. 23A; Perkins, 1984).

Although the broad, spatulatelike condition of paleate setae is most often illustrated, Knight-Jones (1981, 1983) and Perkins (1984) have pointed out that the hooded region is actually very depressed relative to other hood and shaft orientations. The hood is spoon-shaped (Knight-Jones, 1981, 1983; fig. 23B) and the shaft is broadly flattened and slightly curved in cross section (Perkins, 1984). Based on the micrographs of Perkins, the cross-sectional orientation of the paleate setal shaft to lacunae and hood is the same as in broadly hooded setae as opposed to the orientation seen in spinelike setae.

Bayonet setae appear to be a slightly modified form of elongate, narrowly hooded setae (fig. 23D). When present, bayonet setae are aligned in one or two rows, parallel and anterior to other inferior notosetal forms (bay, fig. 19A). Bayonet setae are very short, slen-

der, and straight, or slightly curved. At the point of emergence from the body wall, the shaft may be bent at a slight angle and abruptly tapering. The hood has been illustrated in the past as resembling that of the narrowly hooded condition but has also been shown to appear as “bilimbate,” probably due to orientation when viewed. In some small-bodied species (e.g., some *Oriopsis* spp.), no hood is visible. The limbate condition of bayonet setae may indicate that what appears to be a hood in this setal form may only be a thin layer of asymmetrically distributed microtubules along the shaft, forming a translucent limbation. The cross-sectional pattern of this setal form has not yet been determined.

Bayonet setae have been identified under a variety of names, e.g., basal setae (Southern, 1914, in *Chone*) and capillary setae (Knight-Jones, 1983, in *Oriopsis*). The description of bayonet setae has been infrequent, which has apparently led some workers to consider the character of specific value only (e.g., Bush, 1905; Southern, 1914; McIntosh, 1923). In his work on *Chone* and *Euchone*, Banse (1972) recognized bayonet setae in the generic diagnoses; others have also included it in some generic diagnoses (e.g., Uebelacker, 1984a).

A setal form which initially resembles the paleate form is here referred to as pseudospatulate (fig. 23E, F). This setal type occurs in the *Fabricia-Fabriciolla-Augeneriella* complex as well as in an undescribed genus. Pseudospatulate setae have generally been considered forms which are similar to what are here called broadly hooded or paleate forms. While pseudospatulate setae do resemble paleae in some respects, the mucronate tip of the former is distinctly bent proximally at almost a 90° angle relative to the shaft and appears to be a continuation of the shaft. The lateral, winglike projections on the shaft do not appear to form a hood and are slightly angled away from the direction of the mucro. At this time, however, no cross sections have been made of this form. Pseudospatulate setae are also slimmer than paleae.

The apparent placement of pseudospatulate setae in what is here interpreted to be a single, anterior setal row of inferior notosetal fascicles is supported by the same occurrence of elongate, narrowly hooded setae in other more anterior setigers. This also lends sup-

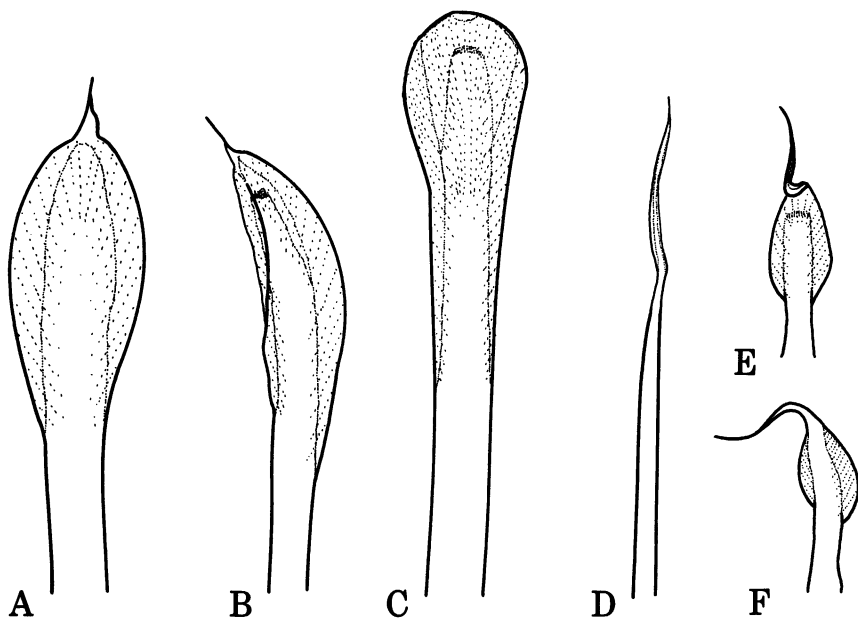


Fig. 23. Paleate setae: A. frontal view, from inferior notopodial row, setiger 3, *Eudistylia vancouveri* (Kinberg) (USNM 44858); B. same in lateral view; C. frontal view, from inferior notopodial row, setiger 4, *Chone infundibuliformis* Kröyer (USNM 41517). Bayonet setae: D. from *Chone infundibuliformis* (after Hartmann-Schröder, 1971). Pseudospatulate setae: E. frontal view, from *Fabricia sabella* (Ehrenberg); F. somewhat lateral view, same.

port to the hypothesis that pseudospatulate setae are not homologous to paleate setae (see below). Thus, relative to pseudospatulate, bayonet, and elongate, narrowly hooded setae, paleate setae only occur as a group in a posterior fascicular row(s).

The superior thoracic notosetal fascicles, which form an arc above the inferior thoracic group, are most commonly composed of elongate, narrowly hooded setae (state 27a), while spinelike (state 27b) and broadly hooded setae (state 27c) are infrequent. Homology of the latter two states with the more common inferior notosetal forms is not necessarily implied.

In the present study, different inferior thoracic notosetal forms in the sabelliforms have been characterized as arising from a distinct anterior and/or posterior region in a fascicle. My intent on making this distinction is to be able to recognize the co-occurrence of several different setal forms within the same fascicle. Designating these anterior and posterior groups (or rows) as separate characters allows for interpretation of putative transformation series in each.

For example, based on outgroup compar-

ison, presence of elongate narrowly hooded setae in inferior thoracic notopodia in *Cao-bangia* would be regarded as plesiomorphic. My interpretation of bayonet setae in *Oriopsis* or *Desdemona* could then follow as being a modification of this state. For taxa such as *Chone*, with anterior row(s) of bayonet setae and posterior rows of paleate setae, there is then the possibility of viewing the paleate state as being added on as a new setal form to the plesiomorphic condition. For the anterior row(s), the plesiomorphic setal condition is that of the outgroup (elongate, narrowly hooded); absence of the second (posterior) setal row(s) or group is also considered plesiomorphic. Such plesiomorphic conditions are based on the view that bayonet setae is one of the states derived from elongate, narrowly hooded setae. This transformation series was also suggested by Rioja (1929). The relationship of these anterior and posterior setal row (or group) transformation series will be presented below.

A particular drawback to this format might be the fact that relative numbers of rows of setae are not taken into consideration when distinguishing "anterior" and "posterior" se-

tal rows or groups. For instance, the Serpulidae can have several rows of elongate narrowly hooded setae per fascicle whereas many fabriciini sabellids have only a single row, and most sabellin genera have two or more rows of paleate setae. One might then argue that it is not possible to distinguish between such rows or groups since there is little or no concordance between number of setal rows. At this time, I know of no solution to the problem of reflecting setal states as well as relative numbers of rows simultaneously and still make the separation between anterior and posterior groups.

In some genera, setal types of the putative anterior row are not consistent along the body. For example, in *Fabricia*, *Fabriciella*, *Auge-neriella*, and Genus B, this anterior (and only) row in setiger 2 always differs from at least three of the more posterior setigers. Thus, the states for anterior and posterior rows of setigers 2 and 4 are used to indicate differences along the thorax. Using only these two setigers avoids redundancy, which would occur if each thoracic setiger was included as a separate character. The anterior row of inferior setae of setiger 2 may include elongate, narrowly hooded (state 28a), bayonet setae (state 28b), or setae may be absent (state 28c).

The elongate, narrowly hooded setae of the serpulids are in a transverse to oblique row as is usually the case in sabellids. In instances where bayonet setae are present but a posterior group or rows of differing inferior setae are absent, bayonet setae are aligned parallel to the lower transverse part of the superior setal arc (see e.g., Wu, 1984, for *Oriopsis*). Setae of the anterior row of setiger 4 include elongate, narrowly hooded setae (state 30a), bayonet setae (state 30d), or setae may be absent (state 30e). In addition, broadly hooded (state 30b) or pseudospatulate setae (state 30c) may be present. Posterior setal row(s) in setigers 2 and 4 (characters 29 and 31, respectively) each have the same possible states: setae absent (a), broadly hooded (b), paleate (c), or spinelike (d).

ABDOMINAL NEUROSETAL CHARACTERS

The abdominal neuropodia can display six possible setal forms. Of these, three appear similar to those of the thorax: elongate, narrowly hooded; spinelike; and paleate. The re-

maining three forms will be described and distribution of these states in characters 32–35 discussed.

Among the Serpulidae, abdominal neurosetae are of two major types: bladelike (sensu Knight-Jones, 1981) and elongate, needlelike (fig. 24A). Bladelike setae occur in various forms (see ten Hove and Wolf, 1984) but consistently have a flattened, bladelike distal end which is usually serrated to some degree along one edge. The “blade” may be very short and distally rounded, or moderately elongate and pointed. A hood or limbation is not present. In the serpulid genera examined, bladelike setae are present in anterior abdominal setigers, forming a single row per fascicle. In posterior abdominal setigers, bladelike setae are abruptly replaced by elongate, needlelike setae which also emerge as a single row in a fascicle. According to T. H. Perkins (personal commun.), needlelike setae extend into anterior abdominal setigers in the serpulid *Sclerostyla* Mörch. This latter setal form is characterized by having a very elongate, narrow shaft, gradually tapering to a fine point. The shaft is slightly curved and lacks a hood.

The decision of polarity for sabellid abdominal neurosetae then becomes more difficult. As a matter of general similarity, the elongate, needlelike form, which lacks a hood, is most easily viewed as the state from which a transformation series of sabellid abdominal neurosetae could be derived. This is especially the case with regard to the derivation of modified, elongate, narrowly hooded setae (fig. 24B) in the sabellids; occurrence in some sabellid genera is consistent with a number of other plesiomorphic characters. The Sabellariidae, as a sister group to the Sabellidae-Serpulidae clade (fig. 3), have abdominal neurosetae resembling elongate, needlelike and narrowly hooded setae in general dimensions but have minute, spiraled serrations extending up the shaft (e.g., Knight-Jones, 1983; Uebelacker, 1984b).

In the current study, the elongate shaft of abdominal neurosetae is considered plesiomorphic. Thus, the elongate, needlelike state of serpulids is plesiomorphic, from which may be derived the modified, elongate, narrowly hooded state in some sabellid genera. The distribution of this latter setal type in a single



Fig. 24. A. Abdominal neuropodial needlelike setae, setiger 50, *Protula diomedeeae* (USNM 3832). B. Abdominal neuropodial modified, elongate, narrowly hooded seta, *Fabriciella trilobata* Fitzhugh (after Fitzhugh, 1983). Elongate, broadly hooded setae: C, D. from posterior and anterior neurosetal rows, respectively, setiger 20, *Pseudopotamilla oculifera* (Leidy) (USNM 5186); E. from anterior neurosetal row, setiger 15, *Schizobranchia insignis* Bush (USNM 40333); F. from posterior neurosetal row, setiger 20, *Laonome kroyeri* Malmgren (NRS 6809).

row within a fascicle is also believed to be the plesiomorphic condition. Two or more rows of setae per fascicle usually arranged in anterior and posterior groups, as present in most sabellid genera, is an apomorphic state (neurop, fig. 20B, C). Based upon comparisons with other character states, the original single row is posterior to an added apomorphic anterior row. This posterior row usually contains modified, elongate, narrowly hooded setae. Each anterior and posterior setal group within a fascicle is regarded as a character. This distinction between anterior and posterior rows or groups in the abdominal neuropodia is somewhat similar to what was attempted for inferior thoracic notosetal fascicles.

In the Sabellidae it is common for setae of

anterior abdominal setigers to differ from those in the posterior part of the abdomen. For this reason, the types of setae in anterior and posterior fascicular rows will be distinguished for anterior and posterior setigers. Transitional patterns in median abdominal setigers have yet to be investigated.

Modified, elongate, narrowly hooded setae (fig. 24B) have what appears to be a very narrow, elongate hood (limbation?). The hood begins just above the point where each seta emerges from the body wall, is widest proximally, and gradually narrows distally. The hood is situated along the convex side of the curved shaft but it is difficult to determine if the hood continues to the end of the shaft. Although the orientation of shaft and hood in cross section is not yet known, it appears

to be similar to that seen in elongate, narrowly hooded setae. Furthermore, the term "hood" may not be appropriate in this case since the presence of internal lacunae has not yet been ascertained; "limbation" might be a more accurate description.

Elongate, broadly hooded setae (fig. 24C–F) appear to be intermediate between thoracic broadly hooded setae and elongate, narrowly hooded setae. The emergent part of the shaft proximal to the hood is short and straight; the hooded region of the shaft is slightly curved and gently tapers to a fine, drawn out tip. The hood is usually abruptly expanded proximally and is widest in this area or somewhat distally. The distal region of the hood narrows and may terminate well below the distal end of the shaft (fig. 24C, E, F). The hood appears to be very thin-walled and usually displays few surface striations. Knight-Jones (1981: fig. 51) presented an SEM micrograph of this form showing the extensive lacunar space between the hood and shaft. The relationship of the shaft and hood in cross section is unknown but appears to be similar either to that of elongate, narrowly hooded or broadly hooded. The distribution of elongate, broadly hooded setae at the generic level is poorly known. Recognition of this setal form in some species other than the type is sometimes ambiguous in that setae of some species appear to more closely resemble the elongate, narrowly hooded form or an intermediate of the two types (Knight-Jones, 1983; personal obs.).

The anterior fascicular row of setae from the anterior abdominal region (character 32) may be absent (state a) or the following setal types may be present: elongate, narrowly hooded (state b; fig. 22A, B), paleate (state c; fig. 23A–C), spinelike (state d; fig. 22C, D), or elongate, broadly hooded (state e). Posterior setal rows in the anterior abdominal region (character 33) may possess elongate, needlelike setae (state a); modified, elongate narrowly hooded (state b); elongate, narrowly hooded (state c); spinelike (state d); elongate, broadly hooded (state e); or setae may be lost (state f). The anterior setal row(s) in the posterior abdominal region (character 34) may be absent (state a) or the following setae may be present: modified, elongate narrowly hooded (state b); elongate, narrowly hooded

(state c); paleate (state d); spinelike (state e); or elongate, broadly hooded (state f). The posterior row(s) of setae in this region (character 35) may be elongate, needlelike (state a); modified, elongate, narrowly hooded (state b); elongate, broadly hooded (state c); or absent (state d).

THORACIC NEUROSETAL CHARACTERS

The thoracic neurosetae of all Serpulidae and most Sabellidae include uncini (sensu Fauchald, 1977). Some sabellid genera also have companion setae (sensu Fauchald, 1977) in these tori (described later). Uncini are arranged side by side in a transverse line in a torus relative to the long axis of the body, with the dentate distal end directed anteriorly. All sabellid thoracic uncini differ from those of serpulids in possessing a large, distal main fang surmounted by a broad series of smaller teeth (fig. 25C, D). In addition, the proximal region of each uncinus extends back as a narrow, rounded handle or shaft (apparently lost in *Laonome* Malmgren). Serpulid thoracic uncini are characteristically compressed into a quadrangular, platelike structure with teeth arranged in a single row (saw-shaped uncini sensu ten Hove and Wolf, 1984) or in several vertical rows (rasp-shaped uncini sensu ten Hove and Wolf, 1984; fig. 25A).

Traditionally, sabellid uncini have been classified as two types: acicular and avicular. Acicular uncini have long handles which are gently curved, proximal extensions of the distal, dentate end (e.g., fig. 25C). Avicular uncini are characteristically Z-shaped or swan-shaped; the handle is sharply bent below the main fang with the proximal part of the handle oriented about 90° relative to the distal part (fig. 25D).

An additional uncinal type has been recognized by Jones (1974a) for *Caobangia*, referred to as palmate hooks. Jones described the hooks as occurring only in the neuropodia of setiger 1. The distal end possesses a central fang encircled by a series of 4–15 teeth. The proximal shaft is round in cross section and straight. As in most sabellids, the thoracic notosetae of *Caobangia* are arranged in two groups: a superior arc and a transverse group of inferior setae (fig. 25F). This condition was

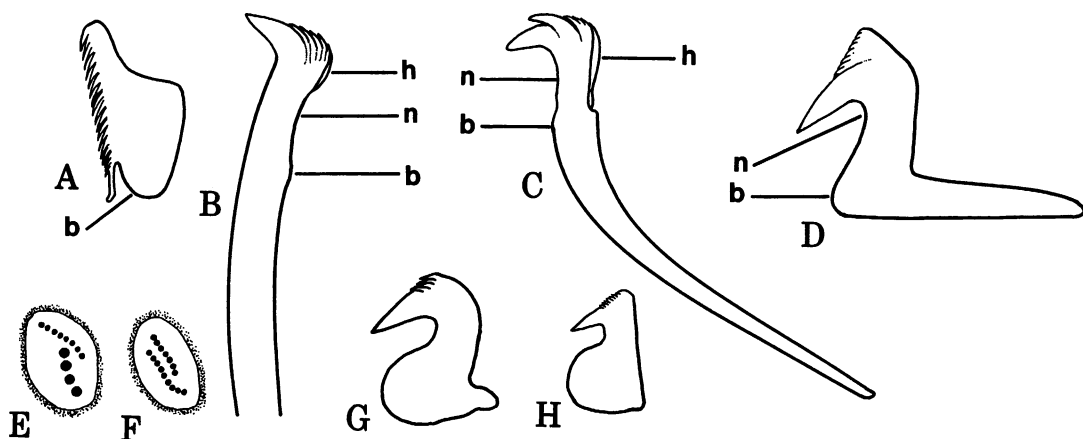


Fig. 25. Thoracic neuropodial uncini: A. from *Protula tubularia* (Montagu) (after Day, 1967); B. distal end, *Chone infundibuliformis* Kröyer (after Hartmann-Schröder, 1971); C. from *Fabriciola trilobata* Fitzhugh, setiger 5 (after Fitzhugh, 1983); D. generalized sabellid avicular uncinus. E. Schematic of setiger 1 notosetae emerging from body wall in *Caobangia brandti* Jones (USNM 50857); superior arc of elongate, narrowly hooded setae, inferior oblique row of palmate hooks. F. Schematic of setiger 3 notosetae from specimen in E; superior and inferior setal groups are elongate, narrowly hooded setae. Thoracic neuropodial uncini: G. from *Branchiomma nigromaculata* (Baird) (after Jones, 1962); H. from setiger 6 of *Laonome kroyeri* Malmgren (NRS 6809).

noted by Jones for setigers 2–7 (Jones, 1974a: fig. 10). Examination of specimens of *Caobangia* indicate that the palmate hooks are not neuropodial in origin but are an inferior group of notosetae (fig. 25E); the position of the hooks does not differ from that of other inferior notosetae. Unlike the elongate handles of acicular uncini, palmate hooks are straight and not subdistally expanded (i.e., with a breast). Thus, the caobangiids have lost the thoracic uncini, which suggests that setiger 1 can be considered to have the typical “collar” setae which are homologous to those of other sabellids and serpulids.

Interestingly, the dentition of the palmate hooks roughly resembles that seen in the region of the basal boss (sensu ten Hove and Jansen-Jacobs, 1984) of some serpulid “collar” setae, except that palmate hooks lack the elongate distal blade. I am hesitant to go so far as to include this condition in the present analysis as homologous to the modified collar setae seen in most serpulids since it has not yet been determined how collar setal forms are distributed throughout the Serpulidae. For example, some of those serpulid genera which were viewed as being plesiomorphic by ten Hove (1984) have collar setae which are either elongate, narrowly hooded (*Protula* Risso,

Apomatus Philippi), or only slightly modified from this form (*Salmacina* Claparède; ten Hove and Wolf, 1984).

Discussion of the phylogenetic or systematic significance of the different sabellid uncini has been infrequent. Rioja (1929) did consider acicular uncini to be primitive due to their similarity to setal forms in the Trichobranchidae. With respect to systematics and phylogenetics, however, the terms “acicular” and “avicular” are vague descriptions which have not been very informative for denoting strict transformation series. This general problem was recognized by Rosenfeldt (1982) for general uncinal transformations and by Holthe (1986) for terebellomorph uncini. Both authors attempted to alleviate this problem by recognizing putative evolutionary changes in parts or areas of each uncinus. A similar approach is taken here for systematic reasons.

Each sabellid and serpulid uncinus is viewed as consisting of four different uncinal characters. The terminology used here is taken from various sources but has generally been consistent with respect to application to sabellid systematics (e.g., Knight-Jones, 1981).

The thoracic uncinal teeth of the serpulids are in a saw-shaped or rasp-shaped arrange-

ment, of equal size, and without a main fang (state 36a; fig. 25A). In the Sabellidae, the distal part of the uncini possesses a large main fang, above which is a broad series of smaller teeth somewhat irregularly arranged in an overlapping pattern, not a uniform set of rows. The teeth above the main fang are usually of equal size (state 36b; fig. 25B, D, G, H) but in some genera there is a distinct, large tooth above the main fang followed by the more typical series of smaller, subequal teeth (state 36c; fig. 25C). This enlarged tooth has been noted by various workers (e.g., Day, 1967; Jones, 1974b; Ben-Eliahu, 1975; Fitzhugh, 1983; Gambi et al., 1983; Wu, 1984). Day (1967) illustrated this tooth as being situated medially above the main fang whereas others have noted that the tooth is slightly offset to one side. This latter condition appears to be the most common (personal obs.). The systematic importance of this character state has not been determined before but appears to be generically consistent.

Proximal to the dentate region of sabellid thoracic uncini is a narrow neck which leads to an inflated area distal to the handle (when present), referred to here as the breast (n, b, fig. 25B–D). Structures equivalent to the neck and breast in serpulid thoracic uncini are difficult to determine with certainty. Many saw- or rasp-shaped uncini possess a narrow process slightly behind the lowest row of teeth, which is set off from the teeth by a distinct notch or groove, but is continuous with the region behind the teeth (b, fig. 25A). Preliminarily, this process is interpreted as being homologous with the sabellid uncinal breast and the notch as representing the neck region (state 37a).

The presence of this poorly developed breast appears in acicular uncini as a slight swelling just proximal to the neck (b, fig. 25B, C). In some sabellid genera, the breast is much larger, extending forward in the same direction as the main fang (state 37b; b, fig. 25D, G, H). The distal margin of the breast is rounded and accentuates the Z-shaped appearance of avicular uncini. The handle is always situated at about a 90° angle to the neck when the breast is well developed.

A handle (or shaft) is absent in the saw- or rasp-shaped uncini of serpulids (state 38a). In the sabellids, the handle is a proximal con-

tinuation of the breast and may be very long (state 38b; fig. 25C), of medium length (state 38c; fig. 25D), or very short (state 38d; fig. 25G). Loss of the handle has presumably occurred in *Laonome* (state 38a; fig. 25H). Very long handles proximal to the breast may be slightly curved or straight, whereas those which are shorter are always straight.

In the region behind the teeth and directly opposite the main fang may be a hyaline structure which was referred to as a hood (state 39b; h, fig. 25B, C) by Uebelacker (1984a). The length of this hood is variable, either covering only the distal area just behind the main fang and teeth, or extending down the neck to near the breast. The hood is apparently composed of a thin layer of microtubules which are separated from the main shaft by a lacunar space. This hood is restricted to acicular uncini of some sabellid genera and appears to be generically consistent (personal obs.), although most workers have not illustrated it.

Companion setae, situated in a row parallel and anterior to the uncini (comp, fig. 19B), may also be in the neuropodial tori. Such setae, also referred to as pick-axe or pen-noned setae, are composed of two distinct regions: a long, slender shaft which is straight or slightly curved distally and a thin, hyaline membrane or mucro at the distal end of the shaft (fig. 26A–C). These distal appendages are probably composed of a thin layer of microtubules. Perkins (1984) has suggested that the membrane may be a continuation of the thin outer covering of the shaft. The shafts lie in the body parallel to the uncinal handles and only the distal ends are emergent. The distal ends of some forms are bulbous and dentate with a main fang (or beak, sensu Perkins, 1984) surmounted by a series of small teeth (state 40b; fig. 26A). Perkins (1984) noted the similarity of this structure to acicular uncini. A hyaline mucro extends from the upper margin of the main fang.

The other type of companion seta is one in which the distal end of the shaft is surmounted by a hyaline membrane oriented perpendicular to the shaft. The attached proximal part of the membrane is wider than the shaft. Of those examined with SEM (e.g., Knight-Jones, 1981) the upper surface of the membrane does have a series of very minute

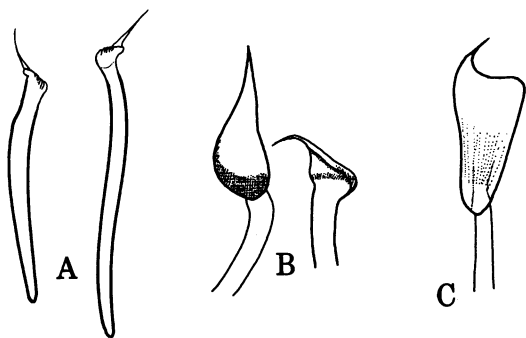


Fig. 26. Companion setae: **A.** from *Demonax microphthalmus* (Verrill) (after Perkins, 1984); **B.** from *Megalomma heterops* Perkins, viewed from above and laterally (after Uebelacker, 1984a); **C.** from *Bispira melanostigma* (Schmarda), viewed from above (after Uebelacker, 1984a).

teeth which could be homologous to the larger teeth and main fang construction just described. In one form, the membrane is roughly symmetrical and teardrop-shaped, with the distal end terminating to a point (state 40c; fig. 26B). The other type is a large, very asymmetrical membrane in which the proximal region is rounded, then widens distally. The distal margin is relatively even, with one corner rounded and the other drawn out to a fine point (state 40d; fig. 26C).

In the past, companion setae have been regarded as valuable systematic characters mostly at the specific level (e.g., Uebelacker, 1984a). The generic revisions of Knight-Jones (1983), Perkins (1984), and Perkins and Knight-Jones (in press) have pointed out the importance of companion setal structure at the generic level. It is, however, important to note that interpretation of shapes, especially of the membranous distal end, is dependent on close control of the angle under which the setae are viewed. Viewing membranes di-

rectly from above, as opposed to laterally, gives a more accurate outline of the shape. Applying pressure to the coverslip of prepared mounts to make the shaft more visible through the body wall will often distort the distal end. This should be avoided until the distal end has been examined.

ABDOMINAL NOTOSETAL CHARACTERS

Abdominal notosetal uncini vary more in shape than do thoracic uncini but the general structural components are the same in both. Generally, two uncinal types have been recognized: rasp-shaped and avicular. Rasp-shaped uncini are relatively similar to those seen in serpulids. They are laterally compressed plates with a quadrangular outline (fig. 27A). Teeth are limited to one margin and are usually of roughly similar (or equal) size. Use of the term "avicular" for abdominal uncini is misleading since a large number of genera possess abdominal uncini without a proximal handle. Apparently, similarities in dentition and breast development have been reasons for use of this term. Like thoracic uncini, abdominal uncini can be regarded as comprising a number of covarying characters.

The plesiomorphic condition for uncinal teeth is that of a rasp-shaped arrangement (state 41a; fig. 27A, B). In this state, teeth are usually of equal size and no main fang is present. In some sabellid genera, however, there are species which do have a single, slightly larger tooth in the lowest row. The more typical sabellid uncinal tooth pattern is like that of the thorax, in which there is a main fang surmounted by a broad series of smaller teeth (state 41b; fig. 27C, D).

The breast of rasp-shaped uncini is usually the same as described for serpulids in that it

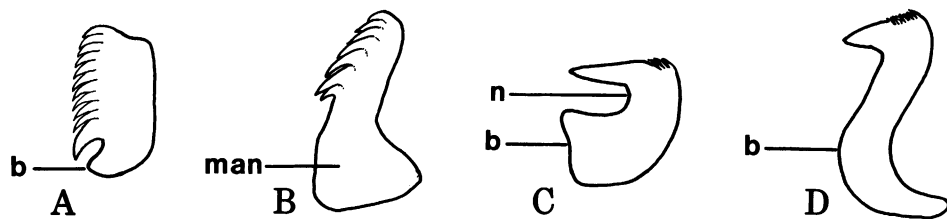


Fig. 27. Abdominal uncini: **A.** from *Oriopsis ehlersi* Day (after Day, 1967); **B.** from *Fabriciella trilobata* Fitzhugh (after Fitzhugh, 1983); **C.** from *Chone infundibuliformis* Kröyer (after Banse, 1972); **D.** from *Potamethus filiformis* Hartmann-Schröder (after Knight-Jones, 1983).

is a small, rounded process below the teeth (state 42a; b, fig. 27A). A modification of this breast occurs in some genera in which the breast extends downward, parallel with the dentate margin, as a large, flattened manubrium (state 42d; man, fig. 27B). In uncini with a main fang, the breast may be well developed and expanded as seen in thoracic uncini (state 42b; b, fig. 27C). In this case, the breast margin below the main fang may be quadrangular, as seen in some *Chone*, or rounded. In some genera with a proximal handle, the breast is very reduced, usually represented only by a slight swelling below the neck (state 42c; b, fig. 27D).

Handles are absent in the saw- or rasp-shaped abdominal uncini of sabellariids and serpulids, and the rasp-shaped uncini of sabellids (state 43a). In abdominal uncini with a main fang, a handle may be present in which case it is either long (state 43b; fig. 25D) or short (state 43c; fig. 25G). The handle is always straight and usually oriented at a 90° angle to the neck.

Phylogenetic and/or systematic considerations of sabellid genera have usually been based in large part on abdominal uncinal form. Rioja's (1929) claim of *Myxicola* being the most primitive sabellid genus was based partly on the presence of uncini apparently resembling those present among the terebellids. The rasp-shaped uncini of other genera were also considered primitive. Banse (1957, 1970, 1972) noted that the rasp-shaped condition of some sabellid genera could be viewed as evidence of the primitive nature of the Fabriciinae since similar uncini are found in the Serpulidae. Banse (1957) also considered the elongate manubrium of some rasp-shaped uncini (state 42d) to be a derived feature.

CHARACTERS NOT INCLUDED IN THE ANALYSIS

The following characters have in the past been considered reliable generic characters and/or used in phylogenetic considerations. These characters are listed below and problems associated with each are discussed in relation to the present analysis.

Several genera have been defined in part on the spiraled condition of the radioles (see e.g., diagnoses of Fauchald, 1977). The spi-

raled condition occurs when the ventral margins of the branchial lobes continue growing, adding radioles, and spiraling along the inner margin of the crown (Perkins, 1984). In the recent revisions of Perkins (1984), and Perkins and Knight-Jones (in press), it has been suggested that spiraling is an "ontogenetic" and size-related phenomenon. In small specimens of some species the branchial base is semicircular and begins to spiral ventrally with increase in size. In other instances, species of the same genus which are small when mature never exhibit spiraling.

I do not think Perkins and Knight-Jones are correct in their dismissal of this character on "ontogenetic" grounds. Characterizing patterns of ontogenetic change can have important implications in systematic studies (e.g., Nelson, 1978; Nelson and Platnick, 1981; Wiley, 1981; Fink, 1982; Weston, 1988). I suspect what Perkins and Knight-Jones actually meant by their statements was that in some genera (e.g., *Demonax* Kinberg) spiraling is inconsistent, occurring in some sexually mature species and not others. This condition has apparently arisen independently within a number of species of different genera which precludes its use in the present study.

Within the *Fabricia-Fabriciola-Augeneriella* complex, as well as several closely related, undescribed genera, the number of radioles is constant with only three pairs. Exclusive of this group, the number of radiole pairs appears to be size related and can vary from as low as three pairs to a higher number. At this time, radiole number must be regarded as a meristic character for which there are no "decided gaps" to which transformation series can be given at the generic level. This is not to say that species in the above complex could not be developmentally or historically constrained to producing only three pairs of radioles. Instead, I suggest that if such constraint is to be hypothesized, the degree of variability between genera must be obtained at the specific level. This is necessary in order to establish (if at all possible) at what level in the hierarchy the plesiomorphic state might occur.

For example, it is very likely that the above *Fabricia* complex is a monophyletic grouping (i.e., on the basis of pygidial eyes, pseudo-

spatulate setae, etc.) which is constrained both developmentally and phylogenetically to produce only three pairs of radioles. What is not known at this time is whether limiting growth to only three pairs of radioles was a unique event, common only to this complex or if a more inclusive plesiomorphic ancestor displayed this trait and gave rise to not only this complex but also such genera as *Oriopsis*, with some species having three to five pairs of radioles (e.g., Banse, 1957).

Banse (1957, 1970) regarded the condition of unequal pinnule length along a radiole as a primitive feature. This was apparently based on the fact that the ancestral sabellid may have resembled *Oriopsis* (fig. 9). While this condition is consistent in a number of genera, it is size related in *Chone* and *Euchone*, with large-bodied species displaying all pinnules of equal length. Until sister-group relationships among species in these two genera are resolved and it can then be determined if unequal pinnule length has arisen one or more times, it seems best not to include this condition.

Sabellid genera usually display a distinct constancy of eight thoracic setigers. Similarly, serpulids generally have only seven setigers. Deviation from these values in either direction has been noted in sabellids, commonly as an intraspecific phenomenon. The presence of an aberrant number of thoracic setigers was used by Jones (1962) to characterize his genus, *Pseudobranchiomma*, with four thoracic setigers. Jones noted that several species of *Branchiomma* Köliker resemble *Pseudobranchiomma* in having what appear to be poorly developed lappets and in lacking radiolar eyes. Jones suggested, however, that these species could only be included in *Pseudobranchiomma* if they possess four thoracic setigers. The drawback to this reasoning is that number of thoracic setigers is utilized to define one genus, but not considered in the same capacity for other genera.

As a meristic character, I would predict that number of thoracic setigers is not so discontinuous as to preclude potential overlap between species. This problem is similar to that seen above for number of radioles. In order to consider the potential for using segment number at the generic level it is first necessary to know the variability of this fea-

ture in all sabellid and serpulid species and to coordinate this with systematic relationships. While one might argue that, for example, the majority of sabellids have eight thoracic setigers whereas serpulids usually have seven, commonality is not justification for viewing either condition as being plesiomorphic (cf. Wiley, 1981).

Number of abdominal setigers is usually size related and can vary from as low as two to over 100 in number. Within the genera *Manayunkia*, *Fabricia*, *Fabriciola*, and *Augeneriella*, abdominal setigers remain constant at three. A cursory examination of the literature on small sabellid species indicates that *Oriopsis limbata* (Ehlers) comes closest to this condition, with numbers ranging from four to six (Banse, 1957). An undescribed fabriciin genus, Genus A, which appears related to *Manayunkia* contains individuals with three or four abdominal setigers. As with the other meristic characters discussed above, number of abdominal setigers is still not a character which can be used at the level of this analysis.

Development of ventral glandular regions into distinct ventral shields is common in both serpulids and sabellids. Degree of development appears to be size related. For example, small-bodied species of *Chone* and *Euchone* lack ventral shields, but are well developed in large-bodied species. Rioja (1929) considered the absence of ventral shields to be primitive in the smaller, more errant sabellids. Banse (1972: 461) made the odd statement that species of *Chone* "with ventral shields are more primitive than those with fully glandularized epidermes because reasonably primitive Sabellidae should have shields." This does not agree with his view (1957, 1970; fig. 9) that *Oriopsis* is a primitive genus in light of the fact that it lacks or has poorly developed shields.

In dealing with the entire sabellid complex, development of ventral epidermal glandularization is a qualitative character in which degree of development can be expressed as a continuum. I find it difficult to judge from general appearances alone when glandular areas can or cannot be considered developed enough to be classified as "shields," especially when dealing with such a large taxonomic group. This is not to say that shield

development is not useful at lower levels of generality, in which all taxa have well-developed shields (e.g., Perkins and Knight-Jones, in press).

CLASSIFICATORY METHODS

All cladistic analyses were conducted on a Toshiba T1200 computer. Initial cladograms were constructed with the use of the **mhennig*** command of the MS-DOS program **Hennig86**, version 1.5, developed by J. S. Farris. This command adds taxa in several different sequences and applies branch-swapping to each of the initial trees (Farris, 1988). The **bb*** command was then given, which applies extended branch-swapping to each of the trees retained by the **mhennig*** command. All minimum-length cladograms produced

from these procedures were retained. All apomorphic states of multistate characters were treated as nonadditive. Transformation series and consistency indices for each character were determined using the **xsteps** command with the **h** and **c** options, respectively.

Character states for several genera had to be coded as unknown, denoted by a "?". For example, thoracic uncini in *Caobangia* have apparently been lost, such that it is not possible to apply any of the states for characters 36–38. Complete loss of thoracic uncini precludes treating these characters as independent in this instance; it would be unrealistic to code each of these characters as having been lost in *Caobangia*. Similarly, the incomplete anterior end of the holotype of *Sabellonga disjuncta* made it impossible to code most features of the branchial crown.

RESULTS

GENERAL CLADOGRAM TOPOLOGIES

Sixteen minimum-length cladograms were produced after branch-swapping, each with a length of 154 steps and a consistency index (C.I.) of 57 percent for the 43 characters given in Appendix III. The cladograms will be referred to as 1 through 16, respectively. Presentation of general similarities or dissimilarities between cladograms will be made with respect to seven areas (I through VII) on each (see fig. 28). In all cladograms, areas I and III–VII are composed of monophyletic clades. Area II comprises a group of genera (or grade) in which most genera extend sequentially from the main stem. This area forms the most plesiomorphic section of the clade comprising areas II–VII. Topological changes between each cladogram are relatively minor, being limited to areas II and III, with shifting of genera or clades occurring only within each area.

Areas II and III each display four possible topologies and will be referred to as IIa–IId and IIIa–IIId, respectively. Topological differences between the 16 possible cladograms are due to the co-occurring combinations of these areas. Table 1 presents the relative arrangements of areas II and III for each clado-

gram. Results will be presented according to area.

In all cladograms, the sabellid clade is defined as a monophyletic group on the basis of at least five character states (fig. 28). One of these states, modification of the anterior peristomial ring margin as a narrow, ventral lobe (state 18d) is homoplasious. Modified, elongate, narrowly hooded setae in posterior rows of anterior (state 33b) and posterior (state 35b) abdominal neuropodia is a synapomorphy for the sabellids in general, which essentially denotes the presence of hooded setae in the abdomen as opposed to the nonhooded condition in the Sabellariidae and Serpulidae. The presence of thoracic uncini with a main fang (state 36b) clearly defines the sabellids although thoracic uncini are lost in *Caobangia*. In addition, the presence of a handle on thoracic uncini (state 38b) defines this grouping, albeit the putative handle has been lost in *Caobangia* and *Laonome*.

In addition to these five states, there are three states at this basal node which show ambiguity: condition of the branchial lobes (character 1), presence or absence of a posterior peristomial ring collar (character 19), and presence or absence of a hood on thoracic uncini (character 39). In the apomorphic condition at this node, each of these states would

be synapomorphies, although with subsequent reversals.

Area I (fig. 28) is monophyletic on the basis of two synapomorphies. The nonhomoplasious synapomorphy is the presence of an enlarged proximal manubrium on abdominal uncini (state 42d). The loss of ventral lips (state 12b) also defines this group, but is homoplasious, having occurred also in *Myxicola* and *Amphiglena*. Separation of the branchial lobes (state 1a) may also be a synapomorphy, depending upon resolution of the condition at the basal node to all areas. For the same reason, the hooded condition of thoracic uncini (state 39b) may also be a synapomorphy. *Caobangia* is the most plesiomorphic genus in the clade. Remaining genera are grouped by the flattened condition of the radioles (state 3c), presence of branchial hearts (state 5b), and the anterior peristomial ring margin developed as a membranous collar (state 18b). This group is part of what has traditionally been considered the Fabriciinae. The presence of vascularized, ventral filamentous appendages (state 14c) may also be a synapomorphy, but there is ambiguity as to the condition of this character in this clade (see fig. 28).

Within area I, *Manayunkia* and Genus A are sister taxa on the basis of the minutely wrinkled appearance of the branchial crown surface (state 2b). A sister-group relationship among remaining genera (*Fabriciola*, Genus B, *Fabricia*, *Augeneriella*) in this area is defined by the presence of pygidial eyes (state 26b) and the unequal size of teeth above the main fang of thoracic uncini (state 36c). The latter synapomorphy (state 36c) is homoplasious, being also found in *Oriopsis*.

The stem leading to area II (fig. 28) and the remaining sabellid genera is defined by six states: presence of a branchial crown radiolar skeleton (state 4c) with two rows of cells, presence of radiolar flanges (state 7b), presence of ventral radiolar appendages (state 15b), presence of the glandular girdle on setiger 2 (state 20b), and presence of thoracic bayonet setae (states 28b and 30d). This area consists of remaining genera traditionally considered in the Fabriciinae, as well as the Sabellinae genus *Potamethus*.

It should be noted that the present cladograms hypothesize two independent acqui-

sitions of the branchial crown skeleton: in *Caobangia* and as a synapomorphy for all genera in areas II–VII. Because of the ambiguity of character 19, the posterior peristomial ring collar, it is possible that presence of this collar (state 19a) is a homoplasious synapomorphy, arising on the stem between *Desdemona* and *Oriopsis*. If this is the case, then the lack of a collar in genera of area I, and *Desdemona*, is a plesiomorphic condition (state 19b). Areas IIa–d differ only in the relationship of the *Jasmineira*–*Panousea* clade to *Chone*1 and *Euchone* (figs. 28, 29). Note that in all cases, *Chone*1 is more closely related to *Euchone*.

Areas III–VII form a monophyletic group in all cladograms on the basis of three states (fig. 28). One of these states is a reversal: loss of the glandular girdle (state 20a). Additional synapomorphies include reduction of the thoracic uncinial handle from the very long form (state 38b) to a medium length (state 38c) and transition of the posterior row of anterior abdominal neurosetae to elongate, narrowly hooded (state 33c).

Area III is well defined by a number of synapomorphies (fig. 28). These include the presence of interramal eyespots (state 21b), inferior thoracic notosetal fascicles in bundles with longitudinal setal rows (state 23b), and abdominal neuropodial tori in the form of conical lobes (state 24b). In addition, genera in area III display thoracic (states 29d, 31d) and abdominal (states 32d, 34e) setae which are at least in part spinelike. An additional synapomorphy in areas IIIa and IIIc, d is the presence of partially spiraled abdominal neurosetal fascicles (state 25b; figs. 28, 30). State 25b is further modified in *Sabella* to a completely spiraled condition (state 25c). For area IIIb, the nodal condition may be states 25a, b, or c, with subsequent changes following accordingly (fig. 30A).

Areas IIIa–d (figs. 28, 30) differ in the placement of *Bispira* and *Sabellastarte*. *Branchiomma* and *Pseudobranchiomma* are sister taxa in all areas, defined by the short handles of thoracic (state 38d) and abdominal (state 43c) uncini. The presence of stylodes (either state 8b or c) may be a synapomorphy in some cases. In areas IIIa and c, *Sabella* and *Bispira* are sister taxa based at least on the presence of companion setae with a distinctly

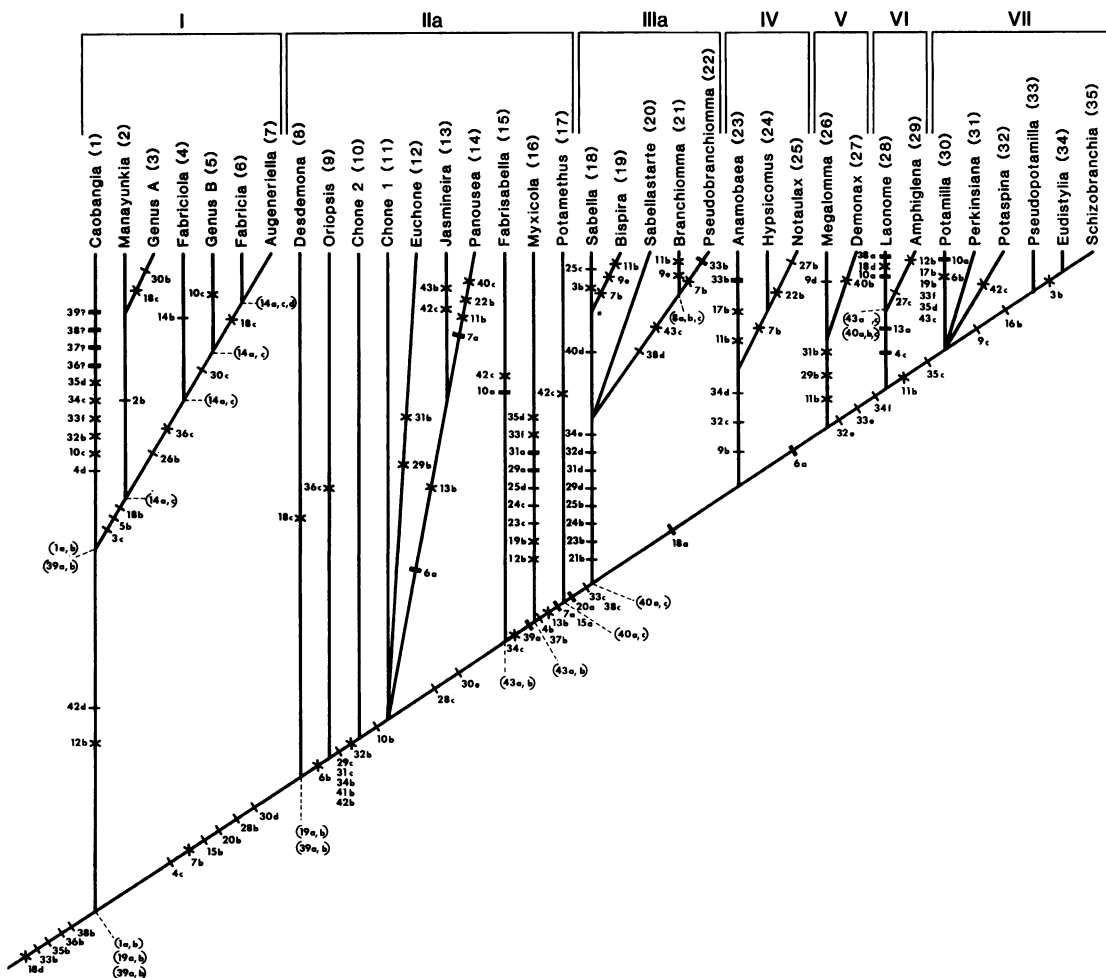


Fig. 28. Cladogram 1 (one of 16 minimum-length cladograms), with areas designated above taxa (see Results for explanation). Genera are numbered for reference to figures 29, 30, and 33. Character state changes are given on stems: single slashes are synapomorphies, x's are homoplasies, dark rectangles are reversals. Characters and states in parentheses at some nodes indicate ambiguity as to which state is possible. The "*" at the node leading to *Sabella* and *Bispira* refers to the possibility of character 33 having states c, d, or f on this stem.

asymmetrical membrane (state 40d). Areas IIIa and d are similar in that *Sabellastarte* and *Bispira* form respective trichotomies at the base of each clade (figs. 28, 30C). Areas IIIb and c are fully resolved, but with different placements of *Bispira* (fig. 30A, B).

Areas IV–VII (fig. 28) are defined by the reduction of the anterior peristomial ring to the plesiomorphic condition (state 18a). This clade may also be defined by the homoplasious occurrence of companion setae (state 40c).

Area IV (fig. 28) is a clade well defined by the presence of simple radiolar eyespots (state 9b) and paleate setae in the anterior row of abdominal neurosetal fascicles (states 32c, 34d). Within area IV, *Anamobaea* is plesiomorphic to *Notaulax* and *Hypsicomus*, the latter two genera being sister taxa based on the common occurrence of radiolar flanges (state 7b).

Areas V–VII are grouped only by the loss of the palmate membrane (state 6a), which is reacquired by *Potamilla* (fig. 28). Area V

TABLE 1
Distribution of Areas II and III (see fig. 28)
Within Each Cladogram
(Characteristics of each area are
described in the text)

Cladogram	Area II	Area III
1	IIa	IIIa
2	IIb	IIIa
3	IIc	IIIa
4	IIa	IIIb
5	IId	IIIa
6	IIa	IIIc
7	IIa	IIId
8	IIb	IIIc
9	IIb	IIId
10	IIb	IIIb
11	IIc	IIIc
12	IIc	IIId
13	IIc	IIIb
14	IId	IIIb
15	IId	IIIc
16	IId	IIId

contains *Demonax* and *Megalomma*. Characters defining area V include the presence of broadly hooded setae in inferior thoracic neuropodia (states 29b, 31b) and dorsal pinnular appendages (state 11b). Both states are homoplasies.

Areas VI–VII (fig. 28) form a monophyletic group by the occurrence of elongate, broadly hooded setae in the anterior and posterior rows of anterior abdominal neuropodia (states 32e, 33e), and elongate, broadly hooded setae in the anterior rows of posterior abdominal neuropodia (state 34f).

Area VI (fig. 28) contains the sister group of *Laonome* and *Amphiglana*, being defined by reversal of the radiolar skeleton to two rows of cells (state 4c) and loss of parallel lamellae (state 13a). Area VII (fig. 28) is monophyletic based on the occurrence of dorsal pinnular appendages (state 11b) and elongate, broadly hooded setae in all abdominal neurosetal fascicles. *Potamilla*, *Potaspi-na*, and *Perkinsiana* form a polytomy with

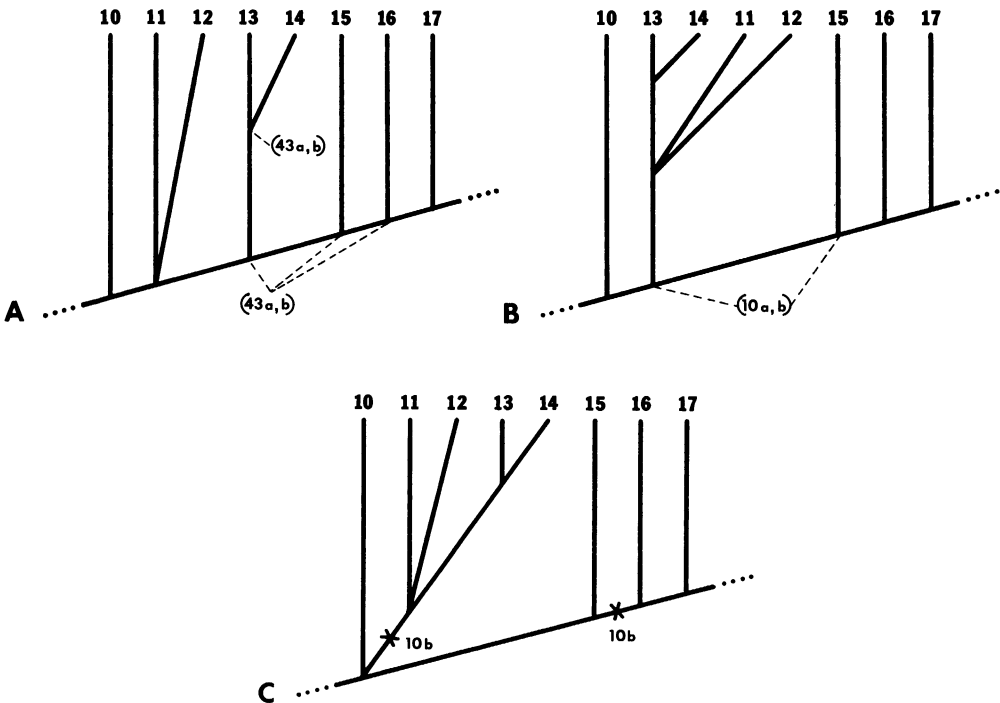


Fig. 29. A–C. Sections of areas IIb, c, and d, respectively, showing possible equally parsimonious topologies. Character state changes are provided only for those states which differ from those seen in figure 28. See figure 28 for explanation of character state changes and table 1 for distribution of areas on cladograms. Genera are numbered as in figure 28.

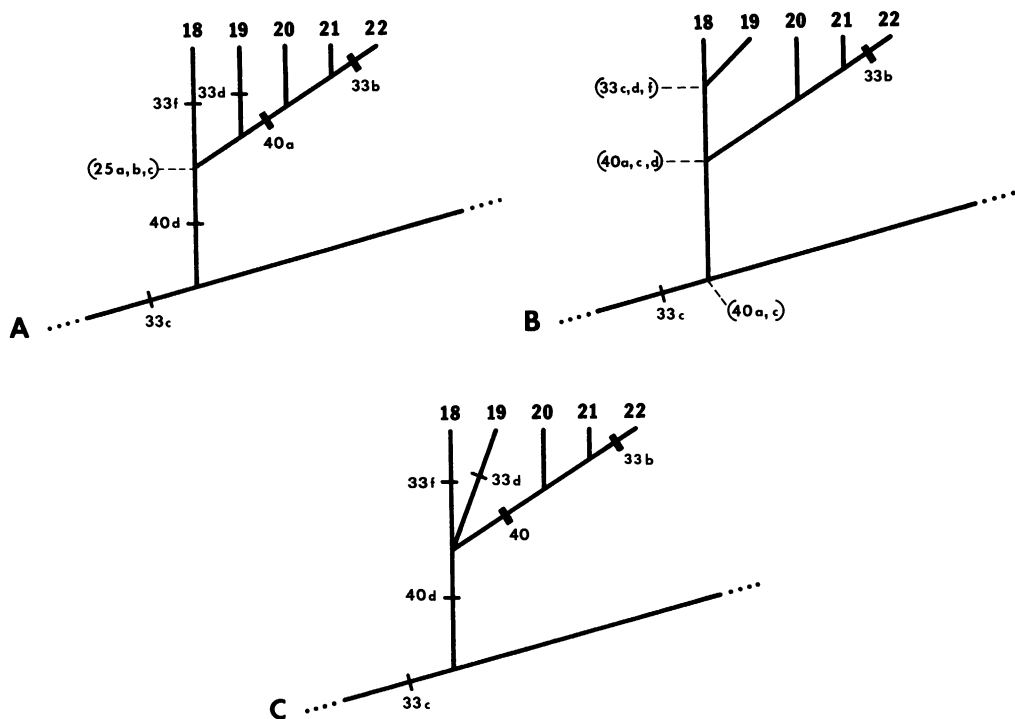


Fig. 30. A–C. Areas IIIb, c, and d, respectively, showing possible equally parsimonious topologies. Character state changes are shown only for states which differ from those seen in figure 28. See figure 28 for explanation of character state changes and table 1 for distribution of areas in cladograms. Genera are numbered as in figure 28.

the *Pseudopotamilla-Eudistylia-Schizobran-*
chia clade. This latter clade is defined by the
presence of unpaired compound radiolar eyes
(state 9c) and dorsal, marginal branchial base
flanges (state 16b).

In the early stages of analysis, *Sabellonga* was included in the data set. The genus is always placed in what is now characterized as area VII. Since all branchial crown structures are unknown, reducing the number of characters present, *Sabellonga* is equally likely to be most closely related to any of the genera in this area. This condition markedly increases the number of possible cladograms, but with no increase in information. Thus, at this time, little useful information is gained from the inclusion of *Sabellonga* except to point out that it is most closely related to sabellid genera of area VII. Character state distributions for *Sabellonga* are presented in Appendix III.

From examination of all taxa for the elucidation and interpretation of characters, it is concluded that Hartman (1969) was ap-

parently mistaken in her interpretation of the anterior end of *Sabellonga disjuncta*. Hartman described two structures on either side of the mouth as palp scars. She noted that a pair of detached palps were present in the sample from which *S. disjuncta* was taken and suggested that the branchial crown of this species had been replaced by spioniform palps. Examination of the holotype of *S. disjuncta* indicates that the structures Hartman interpreted as scars are more likely remnants of, or regenerated, ventral sacs. The structures do not display the typical construction of palp scars. In fact, Hartman's figures are not accurate in this respect. As noted by Hartman, the structures lie on either side of the ventrally placed mouth. Hartman did not note, however, that there is also a pair of small, short lamellae which extend anteriorly from these ventral sacs. The fact that a pair of detached palps was present in the sample is not evidence that they belonged to *S. disjuncta*. It seems likely that this specimen probably had the branchial crown and far

TABLE 2
List of Binary and Multistate Characters Arranged According to Presence or Absence of Homoplasy and/or Reversal Occurring in Transformation Series from Cladograms 1 Through 16

Characters with- out homoplasy or reversals	Characters with reversals only	Characters with reversals and/or homoplasy
Binary		
2	15	1
5	20	6
16		7
21		11
26		12
37		13
41		17
		19
		22
		39
Multistate		
8	38	3
23		4
24		9
25		10
27		14
28		18
30		29
		31
		32
		33
		34
		35
		36
		40
		42
		43

anterior end of the peristomium cropped by a predator. The specimen had, by the time it was collected, regenerated only the ventral sacs, or perhaps these and the remnants of the ventral lips only had time to undergo preliminary wound healing before the specimen was collected. Thus, additional material in which a branchial crown is present must be acquired before further consideration of the genus can be given in this type of study.

CHARACTER STATE
TRANSFORMATION SERIES

Of the 43 characters used in the present study, 19 were coded as binary and 24 were multistate. The transformation series of each

TABLE 3
Number of Steps and Consistency Indices for Binary Characters Displaying Reversals and/or Homoplasy, and All Multistate Characters

Characters	Number of steps	Consistency index (%)
1, 15, 17, 20, 22	2	50.00
3, 36	3	66.66
4, 14, 29, 31, 38	4	75.00
6, 19	4	25.00
7, 11	6	16.66
8, 23, 24, 27, 28	2	100.00
9, 32	5	80.00
10, 43	6	33.33
12, 13, 39	3	33.33
18, 40	7	42.86
25	3	100.00
30	4	100.00
33	10	50.00
34	6	83.33
35	5	60.00
42	6	50.00

character were determined from the final cladograms. Of the 19 originally binary characters, only seven remained strictly binary (C.I. = 100%) on the cladograms while two characters displayed only reversals and no homoplasy. Ten binary characters contained transformation series with homoplasy and usually reversals (table 2). Multistate characters displayed a similar trend; seven characters showed no homoplasy or reversal while one contained only reversals, and 16 characters had both homoplasy and reversal (table 2).

Transformation series for each binary character which displays reversal and/or homoplasy, and all multistate characters, are presented below, especially with regard to how they have determined the types of areas seen on the cladograms. The number of steps and consistency indices for these characters are presented in table 3.

Character 1. Transformation series for this character in all cladograms may take several forms; this ambiguity is indicated in figure 28. Dorsal fusion of the branchial lobes (b) may be a synapomorphy grouping all genera examined, with subsequent reversal to the plesiomorphic state in all genera in area I, except for *Caobangia*. The other possibility

is that the apomorphic condition has arisen as a parallelism in *Caobangia* and all genera in areas II–VII. Thus, lobe separation in remaining genera of area I could be plesiomorphic.

Character 3. The shape of the radioles is relatively uniform in the entire group. The flattened state (c) is a synapomorphy for sabellid genera without a branchial skeleton (in area I). The rounded state (b) is a synapomorphy grouping *Schizobranchia* and *Eudistylia*, but is homoplasious, also occurring in *Sabella*.

Character 4. All cladograms hypothesize the homoplasious origin of the branchial skeleton, occurring in *Caobangia* (d) and as a synapomorphy (c) for areas II–VII. The plesiomorphic condition is maintained in remaining genera of area I. It is interesting to note that this transformation series parallels one of the two possible transformation series seen for character 1 (branchial lobe fusion). From the two-cell row condition (c) is derived the four-cell row state (b) on the stem leading to *Potamethus* (but see diagnosis below) and areas III–VII. A reversal to the two-cell state is one of the synapomorphies grouping *Laonome* and *Amphiglena* (area VI).

Character 6. The palmate membrane (b) is a synapomorphy in area II on the stem between *Desdemona* and *Oriopsis*. It is subsequently lost two times: in the *Panousea-Jasmineira* clade and as a synapomorphy for the clade comprising areas V–VII. The palmate membrane is then reacquired by *Potamilla* (area VI).

Character 7. Radiolar flanges (b) are derived a number of times, being first seen in area II beginning with *Desdemona* but lost in *Panousea* and then on the stem leading to *Potamethus* and areas III–VII. Within area III, flanges are derived independently in *Bispira* and *Pseudobranchiomma*. Flanges are a synapomorphy for the sister-group relationship of *Hypsicomus* and *Notaulax* in area IV.

Character 8. Stylodes in *Pseudobranchiomma* and *Branchiomma* can be hypothesized as derived by three different transformation series in all cladograms: (1) well developed (c) and poorly developed (b) may be derived independently, (2) state b derived from c, or (3) vice versa.

Character 9. All cladograms suggest independent origins for simple (b) and compound eyes (c and d), as well as multiple derivations of compound eyes. The presence of simple eyes is a synapomorphy for genera in area IV (*Anamobaea*, *Notaulax*, *Hypsicomus*). Compound eyes usually limited to proximal regions of radioles (c) is a synapomorphy for the *Pseudopotamilla-Schizobranchia-Eudistylia* clade in area VII. Compound eyes limited to the distal ends of radioles (d) is an autapomorphy in *Megalomma*. The paired compound eyes of *Bispira* and *Branchiomma* (e), although originally considered as homologous states, arise as homoplasies.

Character 10. Dorsal lips have been independently lost (c) in two genera, *Caobangia* and Genus B; the losses occurring from the plesiomorphic condition of lips with no radiolar appendages (a). Dorsal lip radiolar appendages (b) have arisen only once based on cladograms 1–4 and 6–13, in area II on the stem between *Chone2* and *Chone1*. In these cladograms, radiolar appendages have been lost (a) three times; in *Fabrisabella*, *Amphiglena*, and *Potamilla*. Loss of radiolar appendages has also occurred twice in cladograms 3, 5, and 11–16, in *Amphiglena* and *Potamilla*, while derivation of these appendages is possible two times, as a synapomorphy for the *Chone1-Euchone-Jasmineira-Panousea* clade and on the stem between *Fabrisabella* and *Myxicola* (areas IIc and d).

Character 11. The presence of dorsal pinnular appendages (b) appears to be a very labile structure in the sabellids, with numerous independent acquisitions. In all cladograms, pinnular appendages are derived in *Panousea*, *Bispira*, *Branchiomma*, *Anamobaea*, as a synapomorphy for the *Megalomma-Demonax* clade, and as a synapomorphy for all genera comprising area VII.

Character 12. Ventral lips are lost (b) three times: as a synapomorphy for area I, in *Myxicola*, and *Amphiglena*.

Character 13. Parallel lamellae (b) arise two times, as a synapomorphy grouping *Jasmineira* and *Panousea*, and on the stem between *Myxicola* and *Potamethus*. Subsequent loss occurs as a synapomorphy for the *Laonome-Amphiglena* clade (area VI). This structure is also lost independently in *Fabrisabella*.

Character 14. Ventral filamentous append-

ages are present only in genera of area I, exclusive of *Caobangia* and *Fabricia*. Three transformation series are possible in all cladograms. In two transformation series, the unbranched, vascularized state (c) is a synapomorphy grouping all genera except *Caobangia*. From this state are derived the branched, vascularized (d) and unbranched, nonvascularized conditions (b). Loss of ventral filamentous appendages in *Fabricia* may be a derived condition from either state b or d. In the third possible transformation series, all states are derived independently from the plesiomorphic condition (a), with state c being derived independently in the *Manayunkia*-Genus A clade and in Genus B.

Characters 15 and 20. Ventral radiolar appendages (15b) and the glandular girdle (20b) have been derived once, then lost. Both structures originate as synapomorphies for areas II–VII. Ventral radiolar appendages are then lost on the stem between *Myxicola* and *Potamethus* while the glandular girdle is lost on the next stem, between *Potamethus* and areas III–VII. Loss of the glandular girdle is one of the states defining the clade containing areas III–VII.

Characters 17 and 22. The branchial crown ventral basal flanges (17b) and elongate collar setae fascicles (22b) are both homoplasies. The basal flanges are respective autapomorphies for *Anamobaea* and *Amphiglena*, as are the elongate fascicles of setiger 1 in *Panousea* and *Notaulax*.

Character 18. Derivation of the anterior peristomial ring margin as a narrow, ventral lobe (d) is a synapomorphy for all ingroup taxa. This is modified to the membranous collarlike state (b) in area I as a synapomorphy for all genera excluding *Caobangia*. Further modification in area I occurs with derivation of the ventral, wide lobe state (c) in Genus A and the clade containing *Augeneriella* and *Fabricia*. In area II, state d is modified again to state c in *Desdemonia*. Reversal from state d to a is a synapomorphy for areas IV–VII, with subsequent occurrence of state d in *Laonome*.

Character 19. Presence (a) of the posterior peristomial ring collar may be plesiomorphic for the ingroup, or secondarily derived, in all cladograms depending upon resolution of ambiguous character state distributions. In

one case, this collar is hypothesized to have been lost on the stem grouping all sabellids, with this condition being maintained in area I and *Desdemonia*. The collar is then reacquired as a synapomorphy for the remaining sabellid genera on the stem between *Desdemonia* and *Oriopsis*. Subsequent collar loss occurs in *Myxicola* and *Amphiglena*. In the other possible transformation series, possession of the collar is hypothesized to be a plesiomorphic condition for the ingroup, with apomorphic loss occurring independently four times: as a synapomorphy for area I, in *Desdemonia*, *Myxicola*, and *Amphiglena*.

Characters 23, 24, and 27. The transformation series for these characters are completely consistent (C.I. = 100%), with each apomorphic state being derived from the plesiomorphic state. The inferior thoracic notosetal fascicles of most genera are transverse (23a). The apomorphic condition of an irregular setal bundle (23c) is only present in *Myxicola*, while longitudinal rows (23b) is a synapomorphy for the clade comprising area III. Character changes for abdominal neuropodial tori (24) also occur in the same taxa noted above. Superior thoracic notosetae are elongate, narrowly hooded (27a) in all genera except for the independent derivations of spinelike setae (27b) in *Notaulax* and broadly hooded setae (27c) in *Amphiglena*.

Character 25. Abdominal neurosetal fascicles are primarily in the form of one or two transverse rows (a). The apomorphic condition of an irregular bundle (d) is an autapomorphy in *Myxicola*. Two additional states, partially spiraled fascicles (b; present in all genera of area III, except *Sabella*) and completely spiraled fascicles (c; present in *Sabella*), display three possible transformation series. In cladograms 1–16, state c may be derived from b (areas IIIa, c, d). Also, in cladograms 4, 10, 13, and 14 (area IIIb), state b may be derived from c, as well as both states being independently derived from state a.

Character 28. Transformation of the anterior setae of inferior setiger 2 notopodia to bayonet setae (b) is a synapomorphy for areas II–VII in all cladograms. Loss of this setal group occurs on the stem between the *Chone1-Euchone-Jasmineira-Panousea* polytomy and *Fabrisabella*.

Characters 29 and 31. The transformation

series for the posterior rows or group of inferior notosetae of setigers 2 and 4 concern the same setal forms. Paleate setae (c) are derived on the stem between *Oriopsis* and *Chone2*. Broadly hooded setae (b) are present as an autapomorphy in *Euchone*. Spinelike setae (d) are hypothesized to have been derived from paleate setae and are a synapomorphy for the clade comprising area III. The broadly hooded state also occurs in the *Demonax-Megalomma* clade (area V).

Character 30. The plesiomorphic state of the anterior row of inferior setiger 4 notosetae is elongate, narrowly hooded (a). From this is derived the broadly hooded setae (b) of Genus A and pseudospatulate setae (c); the latter defines the Genus B-*Fabricia-Augeneriella* clade in area I. Bayonet setae (d) are also derived from the plesiomorphic state; origin and subsequent loss of this state (e) are the same as seen for character 28.

Character 32. The anterior row of anterior abdominal neurosetae are hypothesized to have originated two times as elongate, narrowly hooded (b): in *Caobangia* and on the stem between *Oriopsis* and *Chone2*. From this latter origin in area II, three states are further derived: spinelike setae (d) as a synapomorphy for area III, the paleate form (c) as a synapomorphy for the clade comprising area IV, and elongate, broadly hooded setae (e) as a synapomorphy for the area VI and VII clade.

Character 33. The plesiomorphic condition for the posterior row of anterior abdominal neurosetae seen in the Serpulidae is elongate, needlelike (a). Within the sabellid clade, the modified, elongate, narrowly hooded condition (b) is derived once from this plesiomorphic state and is a synapomorphy for the sabellid genera. Apomorphic loss (f) from this state has occurred twice, in *Caobangia* and *Myxicola*. The three remaining states are derived from the modified, elongate, narrowly hooded form. Elongate, narrowly hooded setae (c) originate as a synapomorphy for areas III–VII, with subsequent reversal to state b in *Anamobaea*. Transformation series in area III show three possible forms, depending upon resolution of ambiguities. In all cladograms (areas IIIa–d), it is possible for the elongate, narrowly hooded state (c) to change independently to spinelike (d) in *Bispira*, and com-

plete loss (f) in *Sabella*. In cladograms 1–6, 8, 10 and 11, and 13–15 (areas IIIa–c), there is also the possibility of state d transforming to f, and vice versa. Elongate, broadly hooded setae (e) is a synapomorphy for the clade comprising areas VI and VII; however, this state is lost (f) in *Amphiglena*.

Character 34. The anterior row of posterior abdominal neurosetae is apparently derived two different times; as an autapomorphy in *Caobangia*, in the form of elongate, narrowly hooded setae (c), and as modified, elongate, narrowly hooded setae (b) on the stem between *Oriopsis* and *Chone2*. Elongate, narrowly hooded setae (c) are derived from this latter state on the stem between *Fabrisabella* and *Myxicola*. From the elongate, narrowly hooded state are derived three states: spinelike (e), a synapomorphy for the genera of area III; paleate (d), defining the clade of area IV; and elongate, broadly hooded (f), a synapomorphy for the clade comprising areas VI and VII.

Character 35. From the plesiomorphic condition of elongate, needlelike setae (a) is derived the modified, elongate, narrowly hooded state (b) in the posterior row of posterior abdominal neurosetae. The latter state is a synapomorphy for the sabellid genera. This state is hypothesized to have been lost (d) in *Caobangia*, *Myxicola*, and *Amphiglena*. From the modified, elongate, narrowly hooded form are derived elongate, broadly hooded setae (c) as a synapomorphy for area VII.

Character 36. The derived condition of a main fang surmounted by a broad series of equal-size teeth (b) is a synapomorphy for the ingroup. Unequal-size teeth above the main fang (c) is derived from the former state two times; as a synapomorphy for the *Fabriciella*-Genus B-*Fabricia-Augeneriella* clade in area I and as an autapomorphy in *Oriopsis*.

Character 38. The elongate handle (b) of thoracic uncini is a synapomorphy for the sabellid genera. Reduction of the handle to a medium length (c) is a synapomorphy for the clade containing areas III–VII, with further reduction to the short form (d) occurring in the *Branchiomma-Pseudobranchiomma* clade. The medium length handle state is lost (a) in *Laonome*.

Character 39. The hood on thoracic uncini

(b) can be derived one or two times in all cladograms. For multiple origins, the state is a synapomorphy for the clade comprising area I, with the other derivation on the stem between *Desdemonia* and *Oriopsis*. The hood is then lost (a) on the stem between *Fabrisabella* and *Myxicola*. As a single origin, the hood is a synapomorphy for the sabellid genera, with subsequent loss in *Desdemonia* and on the stem between *Fabrisabella* and *Myxicola*.

Character 40. Transformation series for companion setae may take 15 different forms. In general, companion setae with a roughly symmetrical (teardrop-shaped) distal end (c) are derived two or three times: always as an autapomorphy in *Panousea*, and either as a synapomorphy for *Potamethus* and areas III–VII, or with independent derivations in *Potamethus*, area III, and the area IV–VII clade. The distally dentate state (b) arises from state c as a homoplasy in *Demonax* and *Amphiglena*. State b, however, is present in *Amphiglena* either as derived from state c or the secondarily derived state a, due to the sister-group relationship with *Laonome*. The distinctly asymmetrical condition (d) seen in *Sabella* and *Bispira* may be derived from the original plesiomorphic condition (a), from the more symmetrical state (c), or independently derived from the secondary loss of companion setae. The transformation series selected with respect to state c has important consequences for other genera in area III since these latter genera lack companion setae.

Character 42. The small, poorly developed breast of abdominal uncini (a) is present in

Desdemonia and *Oriopsis*. From the plesiomorphic condition is derived the enlarged proximal manubrium (d) in area I. Also from the plesiomorphic condition is derived the well-developed, expanded breast (b) on the stem between *Oriopsis* and *Chone2*. The breast is then modified to the narrow form (c) four times: in *Jasmineira*, *Fabrisabella*, *Potamethus*, and *Potaspina*.

Character 43. Development of a handle in abdominal uncini may occur by four different transformation series in all cladograms. The long-handled state (b) may be derived two or three times. When derived twice, it is found as an autapomorphy in *Jasmineira* and as a synapomorphy on the stem between the *Chone1-Euchone-Jasmineira-Panousea* polytomy and *Fabrisabella*. Loss of the handle is then found in *Myxicola*. In the *Laonome-Amphiglena* clade (area VI), handle modifications may occur independently, with loss (a) in *Amphiglena* and reduction of the handle (C) in *Laonome*. Also, state a or c may be plesiomorphic to the other in this area. A short handle (c) is also a synapomorphy for the *Branchiomma-Pseudobranchiomma* clade in area III. When the long-handled state is derived three times, the general pattern is as above except for the independent derivation of state b in *Fabrisabella*. In cladograms 2 and 8–10, with area IIb, the long-handled state is derived once, on the stem between the *Chone1-Euchone* trichotomy and the *Jasmineira-Panousea* clade. Loss of the handle then occurs in *Panousea*, *Myxicola*, and *Laonome*.

REVISION OF THE SABELLIDAE-CAOBANGIIDAE-SABELLONGIDAE COMPLEX

REVISION OF THE SABELLIDAE

The intent of the present analysis was, in part, to provide empirical evidence that the Sabellidae, as traditionally recognized, is a nondefinable family as a result of being paraphyletic. Within all of the minimum-length cladograms, *Caobangia* and *Sabellonga* fall within the grouping otherwise recognized as the Sabellidae. The monophyletic status of the entire generic complex dealt with here is consistently established in all cladograms by

the presence of (1) thoracic uncini with a main fang surmounted by a broad series of smaller teeth (either as states 36b or c), (2) thoracic uncini with a handle (states 38b–d), and (3) hooded abdominal neurosetae (e.g., states 33b and 35b). The loss of thoracic uncini in *Caobangia* does not present a definitional problem with respect to the monophyly of this complex; such a loss is an autapomorphy for the genus.

Inclusion of *Caobangia* in the above generic complex is supported by a series of sub-

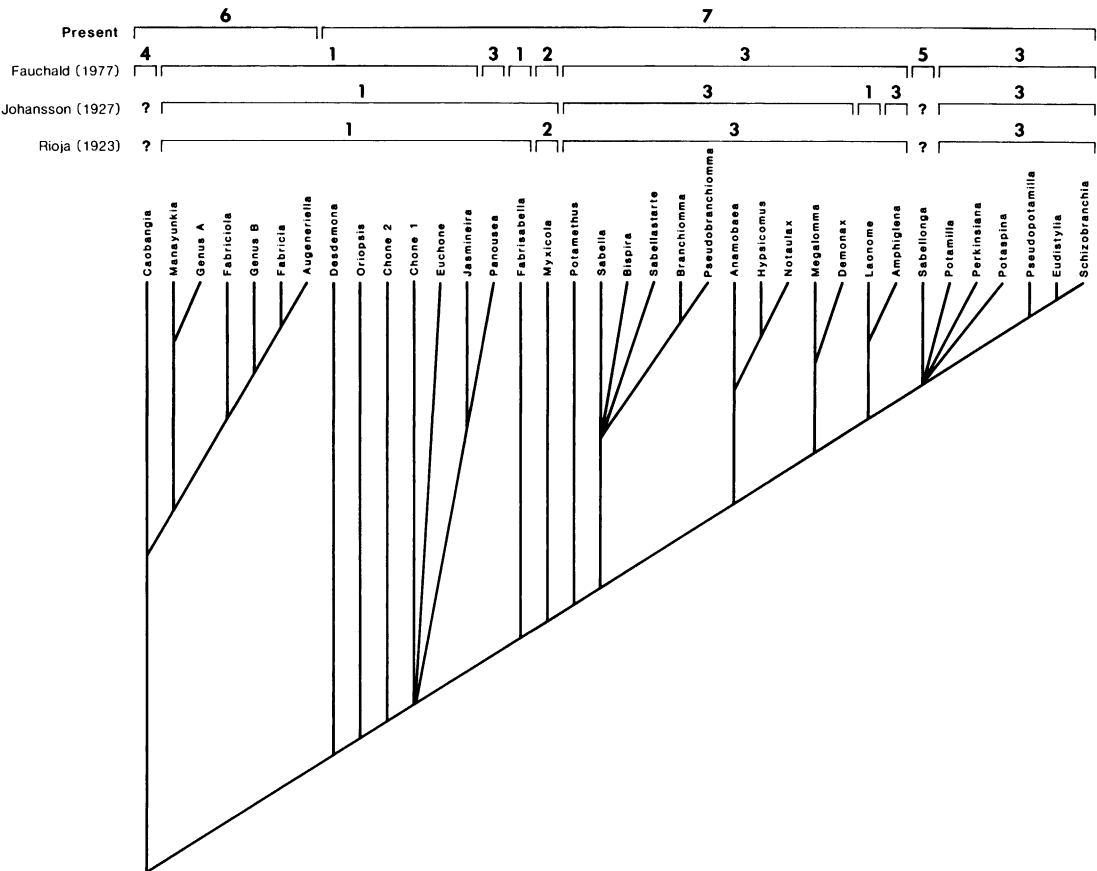


Fig. 31. Adams consensus tree for cladograms 1-16. Families and subfamilies are indicated as designated by Rioja (1923), Johansson (1927), and Fauchald (1977). A revised classification for the group is also provided. Numbers refer to the following taxa: 1 = Fabriciinae, 2 = Myxicolinae, 3 = Sabellinae, 4 = Caobangiidae, 5 = Sabellongidae, 6 = Fabriciinae, revised, 7 = Sabellinae, revised.

sidiary character states generally present in the sabellid group, such as dorsal fusion of the branchial lobes and the manubrium on abdominal uncini. The same situation holds for *Sabellonga*. Revision of this generic complex should aim at establishing monophyletic taxa, yet require minimal change from currently used groupings, invoking minimal redundancy (Wiley, 1979, 1981). This is most effectively accomplished by placing *Caobangia* and *Sabellonga* into the Sabellidae (fig. 31). A diagnosis for the Sabellidae s.l. is provided later.

REVISION OF THE
SABELLIDAE SUBFAMILIES

The commonly used subfamily concepts (reviewed above) of Rioja (1923), Johansson (1927), and Fauchald (1972, in part; 1977)

can now be examined with the results of the cladistic analysis presented above. Figure 31 presents the subfamily distributions on an Adams consensus tree of the 16 cladograms presented in the Results section.

Segregation of the present genera into the subfamilies defined by Rioja (1923) is based primarily on the nature of the thoracic uncinal breast and length of the abdominal notopodial tori. Rioja's use of the terms "acicular" and "avicular" referred primarily to the breast and not so much to handle length. He did not include *Caobangia* in his study and it is difficult to judge how it would fit into his scheme. The recently described genus *Panousea* Rullier and Amoureux presents a problem for this system since acicular thoracic uncini are present in conjunction with companion setae. Exclusive of *Caobangia* and

Panousea, Rioja's Fabricinae is a paraphyletic subfamily due to recognition of the Myxicolinae and Sabellinae (fig. 31). Since the Myxicolinae is monotypic, it is by definition monophyletic; as distinguishing features (at least) may be mentioned the presence of abdominal notopodial tori forming nearly complete cinctures. Some of the defining qualities of the Myxicolinae, however, are simply redundancies of character states recognized at the generic level (e.g., abdominal uncinial tori) or higher (e.g., palmate membrane). While the Sabellinae (including *Sabellonga*) could be considered monophyletic by the presence of avicular thoracic uncini, the Fabricinae is defined by acicular uncini, which is a symplesiomorphy.

Johansson's (1927) subfamily definitions differ from those of Rioja (1923) primarily in that Johansson placed greater emphasis on the length of the thoracic uncinial handle, presence or absence of longitudinal "nematoid" musculature, and nerve innervation of the branchial crown. As a result, Johansson reassigned *Myxicola* to his Fabriciinae. Although Johansson distinguished the Fabriciinae as having long-handled uncini in at least the thorax, he still maintained *Potamethus*, with its long-handled thoracic uncini, in the Sabellinae. Thus, Johansson's definitions were set up such that the three (or four) individual features which were used to define each subfamily were at times in conflict with one another. Resolution of such a problem was apparently made via differential (and unexplained) character weighting (e.g., in the case of *Potamethus*).

Another case in point is the placement of *Laonome*. It was referred to the Fabriciinae by Johansson (1927) since it presumably possessed the primitive condition of "nematoid" musculature and the branchial crown was innervated by two pairs of nerves. Although the thoracic uncini have lost the handle in this genus, they are still most similar to those of the Sabellinae with respect to breast development. The above combination of character states is apparently what led Johansson to conclude that *Laonome* is a transition form between genera of the Fabriciinae and Sabellinae. Unfortunately, the manner in which Johansson's subfamilies are delineated cannot substantiate this hypothesis of relationship.

The distribution of genera within Johansson's subfamilies closely follows that of Rioja (1923) except in the case of *Myxicola* and *Laonome*, which are placed in the Fabriciinae in Johansson's scheme (fig. 31). Johansson, like Rioja, did not consider *Caobangia* in his definitions. Johansson's Fabriciinae is paraphyletic because of recognition of the Sabellinae, the Fabriciinae again being defined by symplesiomorphy. Because of the recognition of *Laonome* as a member of the Fabriciinae, the Sabellinae is also paraphyletic. As noted earlier, Orrhage (1980) has pointed out the inconsistencies of Johansson's subfamily criteria with respect to non-setal characters.

Fauchald's (1977) subfamily definitions essentially followed those of Rioja (1923), although Fauchald recognized the Caobangiidae and Sabellongidae. The problem of distinguishing fabriciin and sabellin genera by exclusive definitions was still not resolved. Fauchald placed *Panousea* in the Sabellinae, apparently only on the basis of the presence of companion setae; the definitional conflict caused by the presence of acicular thoracic uncini and companion setae was not addressed. The implied weighting in favor of companion setae in this instance may have been derived in part from Fauchald's (1972) earlier suggestion of redefining subfamilies only on the basis of presence or absence of companion setae.

The problems seen with Rioja's (1923) scheme are still present in Fauchald's arrangement in that the subfamily Fabricinae is paraphyletic as a result of recognizing the Caobangiidae, Myxicolinae, and Sabellinae, and by placement of *Panousea* in the Sabellinae (fig. 31). Based on the present results, the Sabellinae (sensu Fauchald, 1977) is polyphyletic, with genera being grouped on the homoplasious occurrence of companion setae. This grouping comprises *Panousea* and all genera with avicular thoracic uncini.

While the desire to denote sabellid subfamilies has been spurred, at least in part, by the need to present views of relationship, the criteria by which these categories have been defined are inadequate. The primary drawback to the older subfamily schemes is the inability to define monophyletic groups. This has been due in part to reliance on a small number of characters with states that are often incon-

sistent or are poorly known. Prior to the development of cladistic techniques, very little understanding of the hierarchical nature of character states or recognition of the concept of transformation series can be found in the polychaete literature.

For example, in establishing classifications, past workers have tended to view acicular and avicular uncini as essentially two separate characters or as states which are not considered as parts of a transformation series. This has effectively made treatment of such structures as related entities impossible; i.e., recognition of a transformation series of character states is either not allowed or not recognized. On the other hand, despite the actual treatment of the characters, specific statements concerning character evolution have been couched in terms of transformation series (e.g., Rioja, 1929, 1931; Johansson, 1927). Such an inconsistent interpretation of character data is the primary reason for the Fabriciinae being paraphyletic.

As shown here, there are several concurrent transformation series involved with uncini which have not been acknowledged by past workers as a result of classifying uncini only as avicular or acicular. Further, the fact that no explicit or comprehensive hypotheses of relationship have been presented for the Sabellidae (except, at least partially, by Banse, 1957, 1970; fig. 9) has hindered the establishment of maximally informative subfamilies.

Based on the present results, it is not possible to revise the sabellid subfamilies such that they are both monophyletic and contain a generic distribution similar to that of the original subfamilies. Initially, it might appear more advantageous to establish separate subfamilies for each of the major areas (I–VII) designated on the cladograms in the Results section (fig. 28). There is a drawback to this procedure. While areas I and III–VII are each monophyletic clades, area II, if designated a subfamily, would still be paraphyletic.

The most efficient revision of the subfamilies would appear to be as follows: (1) reduce the Fabriciinae such that it only comprises genera of area I, and (2) expand the Sabellinae to include all remaining genera, including *Sabellonga*. At this hierarchical level, the

pattern of sister-group relationships seen in the consensus cladogram (fig. 31) is exactly reflected in the classification. Diagnoses for the revised Fabriciinae and Sabellinae are given in the next section.

As hypotheses of sister-group relationships, the previous schemes of Meyer (1888), Rioja (1923), and Johansson (1927) are not supported by the present generic relationships. The differences reflect the criteria used in character polarization, and, more importantly, the degree to which higher taxa (families or informal groupings in the case of Meyer, subfamilies of Rioja and Johansson) actually reflected statements of relationship.

For example, Rioja's (1923) subfamily concept was later (Rioja, 1929, 1931) considered as a hypothesis of phylogenetic relationship in which the Myxicolinae is the most primitive subfamily, followed by the Fabricinae, with the Sabellinae being most derived. This statement can only be accepted as an informal judgement about phylogeny in that Rioja's scheme cannot be translated into a cladistic pattern of monophyletic subfamilies: a three-taxon statement (e.g., fig. 8B) can only denote that the Fabricinae and Sabellinae are sister taxa and the subfamily Myxicolinae is plesiomorphic to this grouping. Similarly, the two-taxon statement (fig. 8C) implied by Johansson's subfamilies can only suggest that his Fabriciinae and Sabellinae are sister taxa. This pattern, however, is inconsistent with Johansson's expressed statement that the Fabriciinae should be more primitive than the Sabellinae. I came to a similar conclusion earlier (see above) with regard to a comparison of the phylogenetic views given by Banse (1957, 1970) and his advocacy of Johansson's subfamily scheme (fig. 9).

I would interpret statements by the above workers collectively as an attempt to utilize subfamilies as summary statements about ancestor-descendent relationships, as opposed to denoting sister-group relations. If, however, supraspecific taxa are class constructs (Hull, 1976, 1980) representing historical groupings of genealogically related species, then it is not possible for one subfamily to "give rise," or evolve, into another subfamily (Eldredge and Cracraft, 1980). In a general sense, the phylogenetic statements

of Rioja (1923), Johansson (1927), and Banse (1957, 1970) are corroborated by the present results in that many of the traditionally recognized "fabriciini" genera are plesiomorphic to "sabellini" genera. The present results differ qualitatively, however, from previous studies in that the newly revised subfamilies

reflect a maximally informative hypothesis of sister-group relationship within the revised Sabellidae. While the revised Fabriciinae and Sabellinae are sister taxa, the idea of one being plesiomorphic and the other apomorphic does not hold in two-taxon statements.

CLASSIFICATION OF THE SABELLIDAE S.L.

The following diagnoses are presented for the revised Sabellidae, the subfamilies and genera included in the study. The sequence of taxa given below is meant to reflect, as much as possible, the branching order of taxa in the consensus cladogram (fig. 31). This sequencing procedure is adopted from the "phyletic sequencing convention" of Nelson (1972, 1974) and Wiley (1979, 1981: "Convention 3"). Character states listed in diagnoses include synapomorphies (italicized) for the appropriate taxon as well as additional characters which have been useful in identification at that level.

A definite weakness of these diagnoses is that not all species have been examined from all genera. As such, not all exceptions can be listed. Further, what might actually be an autapomorphy of the type species might be incorrectly included in the generic diagnosis as an assumed synapomorphy. No doubt workers will also complain that certain obvious features have not been included, such as the nature of ventral shields. As I explained earlier, the level at which this analysis has been conducted precludes effective inclusion of some lower-level characters. I would hope that the present analysis will stimulate interest in looking at such features, especially in relation to the nature of the groupings defined here.

For the cladistic analysis, it was assumed that the included genera are monophyletic; thus, generic-level synapomorphies were not taken into consideration at that time unless they were part of a higher-level transformation series. Based on the diagnoses given below, however, the following six genera are nondefinable in terms of being monophyletic taxa: *Chone*, *Sabellastarte*, *Perkinsiana*, *Pseudopotamilla*, *Eudistylia*, and *Schizobranchia*. It is unlikely that the general to-

pology inferred by the present cladograms will be greatly affected by this condition. One of the important points of this section is that the idea of establishing monophyletic taxa has not been extensively considered for polychaetes at the generic (or any other) level.

SABELLIDAE JOHNSTON, 1846, REVISED

DIAGNOSIS: Sabelliform polychaetes which produce a mucoid, gelatinous, or horny tube; may be encrusted with sediment. Tentacular crown with or without skeletal supporting cells. Branchial lobes fused dorsally or completely separate. *Thoracic neuropodial uncini* (absent in *Caobangia*) with *main fang surmounted by broad series of smaller teeth*; subdistal breast present, either as narrow, inflated region or as large, distally directed projection; *proximal region of uncini with handle or shaft* (absent in *Laonome*). *Abdominal neurosetae hooded or appear to have a limbation along shaft*.

REMARKS: As noted earlier, the synapomorphies defining the revised Sabellidae at this time only include (1) the pattern of dentition on thoracic uncini, (2) presence of the handle in thoracic uncini, and (3) the hooded nature of abdominal neurosetae. An additional synapomorphy may be dorsal fusion of the branchial lobes, with subsequent separation in all fabriciini genera except *Caobangia*. There is, however, the equally parsimonious transformation series in which dorsal fusion has occurred two times, in *Caobangia* and as a synapomorphy for the revised Sabellinae.

It is interesting to note that at the generic level, present results suggest independent derivations of the branchial skeleton in *Caobangia* and the Sabellinae. In relation to fused

or separate lobes one might predict, then, that conceivably there is an undescribed taxon with fused lobes and no branchial skeleton, or with separate lobes but with a skeleton. If we insist that there be no independent derivation of the branchial skeleton and lobe fusion, i.e., that both features are necessary correlates, and have a unique derivation, then such features would also be synapomorphies for the revised Sabellidae. This, however, would also necessitate accepting a less parsimonious arrangement of these features with no particular empirical basis for defense.

The majority of definitions of the Sabellidae have been vague owing to the tendency to rely on "Gestalt" in separating the family from the Serpulidae, or else separating the two families by the fact that serpulids produce a calcareous tube. In some instances, the absence of an operculum in sabellids is cited as a defining character. Since some serpulid genera also lack an operculum and there is no evidence to suggest this is a loss (ten Hove, 1984), it is not appropriate to define the Sabellidae or any other group by the absence (as opposed to the loss) of a structure.

FABRICIINAE RIOJA, 1923, REVISED

DIAGNOSIS: Small-bodied sabellid genera with two or three pairs of radioles. Branchial skeleton absent except in *Caobangia*. Branchial lobes separate except in *Caobangia*. *Ventral lips absent*. Anterior peristomial ring always developed along anterior margin either as (1) a narrow, ventral lobe, (2) a thin membranous collar, or (3) a wide, ventral lobe. Posterior peristomial ring collar absent. Inferior thoracic notosetae (interpreted as a single anterior row) usually as elongate, narrowly hooded in at least setigers 1 and 2. Abdominal neurosetae arranged as single row (interpreted as a putative posterior row) of modified, elongate, narrowly hooded setae, except in *Caobangia*. Thoracic uncini (absent in *Caobangia*) acicular, with narrow breast and long handle; hood present. Abdominal notopodial uncini with teeth in rasp-shaped arrangement; *breast modified as elongate, proximal manubrium*; handles absent. Abdominal setigers number 3 to >10.

REMARKS: The revised Fabriciinae is still

somewhat heterogeneous by inclusion of *Caobangia*, limiting the number of synapomorphies for the group. Exclusive of *Caobangia*, the subfamily contains at least six genera which are sister taxa on the basis of presence of branchial hearts, flattened radioles, hoods on thoracic uncini, and (as a possible synapomorphy) separation of the branchial lobes.

CAOBANGIA GIARD, 1893

TYPE SPECIES: *Caobangia billeti* Giard, 1893, by monotypy.

DIAGNOSIS: Small-bodied fabriciina species with three pairs of radioles; radiolar cross section quadrangular in shape; *radiolar skeleton with single row of cells*. Branchial lobes fused middorsally. *Dorsal lips absent*. Anterior margin of anterior peristomial ring appears drawn out as narrow ventral lobe. *Inferior thoracic notosetae of setiger 1 modified as palmate hooks*; inferior notosetae in setigers 2–7 a single row of elongate, narrowly hooded setae. *Abdominal neurosetae composed of single (anterior?) row of elongate, narrowly hooded setae*. *Thoracic neurosetae absent*. *Terminal portion of gut extends anteriorly and dorsally*; anal opening on dorsal surface of anterior thoracic region.

REMARKS: The above diagnosis differs from Jones' (1974a) primarily with respect to interpretation of the palmate hooks and addition of previously undescribed branchial crown and peristomial structures. As noted earlier, the position of the palmate hooks is the same as that of other inferior thoracic notosetae. Also, it is still open to question whether setiger 1 contains the "collar" setae or if this setiger has been lost since there are only seven thoracic setigers. As discussed earlier, I have not interpreted the dentition of the palmate hooks to be the same as the modified collar setae seen in setiger 1 of many serpulids.

MANAYUNKIA LEIDY, 1858

TYPE SPECIES: *Manayunkia speciosa* Leidy, 1858, by monotypy.

DIAGNOSIS: Fabriciina species with *two* (three?, see Remarks) *pairs* of flattened radioles; surfaces minutely wrinkled. Ventral filamentous appendages vascularized, un-

branched. Branchial hearts present. Anterior margin of anterior peristomial ring a membranous collar. Inferior thoracic notosetae a single row, elongate, narrowly hooded or replaced in median setigers by pseudospatulate setae. Thoracic uncini with main fang surmounted by broad series of equal size teeth; hood present. Three abdominal setigers.

REMARKS: *Manayunkia* most closely resembles Genus A in that both have radiolar surfaces which are minutely wrinkled; unbranched, vascularized ventral filamentous appendages; and similar dentition of thoracic uncini.

Traditionally, *Manayunkia* has been defined by the presence of only two pairs of radioles. While examining specimens of *M. speciosa*, I have noticed that there are two pairs of pinnulate radioles; in addition there is a pair of slender, filiform appendages extending from the branchial lobes and situated on either side of the dorsal midline. These structures are unbranched and about the same thickness as the pinnules or ventral filamentous appendages. Zenkevitch (1925) referred to these structures as "dorsal lips," while Pettibone (1953) called them "mediodorsal tentacles." In his description of *M. brasiliensis*, Banse (1956) presented ontogenetic evidence that these structures are pinnules which have migrated out of position with the dorsalmost radioles. In *M. speciosa*, however, pinnules extend from the dorsalmost radiole on the side opposite to these structures and each "tentacle" originates from the branchial lobe itself, not from the dorsalmost radiole. Preliminary observations indicate that this structure is also present on *M. athalassia* Hutchings et al., 1981, but may be absent in *M. aestuarina* (Bourne). Further work needs to be conducted to determine the specific distribution of this structure and to examine the possibility that it is a reduced radiole and not a pinnule.

Since the type species was used in the present study, the presence of inferior thoracic pseudospatulate setae was not taken into consideration in the cladistic analysis. The distribution of this latter setal form was described by Banse (1956) for *M. brasiliensis* as occurring in setigers 2–5. Once revisionary work has been completed for this genus, the question of homology between the pseudo-

spatulate setae of *Manayunkia* and some other fabriciini genera can be better addressed.

GENUS A

DIAGNOSIS: Fabriciini species with radiolar surface minutely wrinkled; three pairs of flattened radioles. Ventral filamentous appendages vascularized, unbranched. Branchial hearts present. Anterior margin of anterior peristomial ring with wide ventral lobe. *Surface epithelium with emergent calcareous spicules; highest concentration in pinnules and ventral surface of setigers 11 and 12 and pygidium.* Thoracic inferior notosetae of setigers 1 and 2 and 7 and 8 elongate, narrowly hooded; *broadly hooded setae in setigers 3–6.* Thoracic uncinal fang surmounted by series of equal size teeth; hood present. Three to four abdominal setigers.

REMARKS: Genus A is very distinctive in that species produce calcareous spicules over the general body surface. At present, specimens belonging to this genus have been obtained from the Indian, Pacific, and Atlantic Oceans. The genus resembles *Manayunkia* in possessing a minutely wrinkled radiolar surface and in the shape of the ventral filamentous appendages and thoracic uncini.

Unlike most genera of the revised Fabriciinae, specimens of Genus A tend to show variation, which may be size related, in number of abdominal setigers. Smaller specimens usually have three setigers while most larger specimens have four. When this last abdominal setiger (setiger 12) is present, it is usually not as long or well formed as other abdominal setigers. At this time, correlations between size, sexual maturity, and number of abdominal setigers have not been made. The holotype of *Augeneriella dubia* Hartmann-Schröder, 1965, has been examined and belongs in this genus (see Remarks on *Augeneriella* below).

FABRICIOLA FRIEDRICH, 1939

TYPE SPECIES: *Fabricia* (*Manayunkia*) *spongicola* Southern, 1921, subsequent designation by Uschakov (1955).

DIAGNOSIS: Fabriciini species with *unbranched, nonvascularized ventral filamentous appendages*; three pairs of flattened radioles. Branchial hearts present. Anterior margin of anterior peristomial ring modified

as low membranous collar. Paired, pygidial eyes present. Inferior thoracic notosetae a single row, elongate, narrowly hooded. Thoracic uncini with main fang surmounted by broad series of unequal size teeth; hood present. Three abdominal setigers.

REMARKS: *Fabriciola* is a part of the clade including *Fabricia*, *Augeneriella*, and Genus B, defined by the presence of unequal size teeth above the main fang of thoracic uncini and pygidial eyes. *Fabriciola* differs from other genera in that it has unbranched, nonvascularized ventral filamentous appendages in combination with a membranous collar on the anterior peristomial ring.

GENUS B

DIAGNOSIS: Fabriciian species in which *dorsal lips are absent*; ventral filamentous appendages unbranched, vascularized. Three pairs of flattened radioles. Branchial hearts present. Anterior margin of anterior peristomial ring with poorly developed collarlike membrane. Pygidial eyes present. Inferior thoracic notosetae of two types (in single row per fascicle): elongate, narrowly hooded in setigers 1 and 2; *pseudospatulate in setigers 3–8*. Thoracic uncinal teeth of unequal size above main fang; hood present. Three abdominal setigers.

REMARKS: Genus B is similar to *Manayunkia*, Genus A, and *Augeneriella* in the presence of vascularized, ventral filamentous appendages, but differs in that the dorsal lips have been lost. In addition, the anterior peristomial ring is produced into a collarlike membrane which is poorly developed only dorsally and barely visible. The distribution of thoracic pseudospatulate setae is unique in being present through setiger 8. The present diagnosis is based only on an undescribed species collected from the Aldabra Atoll, in the Indian Ocean.

FABRICIA BLAINVILLE, 1828

TYPE SPECIES: *Tubularia stellaris* Müller, 1774, by monotypy.

DIAGNOSIS: Fabriciian species in which *ventral filamentous appendages are absent*; three pairs of flattened radioles. Branchial hearts present. Anterior margin of anterior peristo-

mial ring modified to a wide, ventral lobe. Paired pygidial eyes present. Inferior thoracic notosetae of two types (in single row per fascicle): elongate, narrowly hooded in setigers 1, 2, and 8; pseudospatulate in setigers 3–7. Thoracic uncini with unequal size teeth above main fang; hood present. Three abdominal setigers.

REMARKS: *Fabricia* most closely resembles *Augeneriella* and Genus A in the occurrence of a ventral, wide lobed extension of the anterior peristomial ring. *Fabricia* is unique in that the ventral filamentous appendages have apparently been lost.

The type species designation given here differs from that presented by several earlier workers. For example, Bush (1905) appears to be the first to have explicitly designated a type species, *Fabricia fabricii* (Müller), subsequent to Blainville's (1828) description of the genus. Hartman (1951, 1959) and Banse (1956), however, stated that the type species is *F. sabella* (Ehrenberg). Since Blainville (1828) only included *Tubularia stellaris* Müller in *Fabricia*, this species is, by definition, the type species by monotypy. This problem will be addressed in a future revision of *Fabricia* (Fitzhugh, in prep.).

AUGENERIELLA BANSE, 1957

TYPE SPECIES: *Augeneriella hummelincki* Banse, 1957, by monotypy.

DIAGNOSIS: Fabriciian species with *branched, vascularized ventral filamentous appendages*; branching may be simple or compound. Three pairs of flattened radioles. Branchial hearts present. Anterior margin of anterior peristomial ring a wide, ventral lobe. Paired pygidial eyes present. Inferior thoracic notosetae of two types (in single row per fascicle): elongate, narrowly hooded in setigers 1, 2, 7, and 8; pseudospatulate in setigers 3–6. Thoracic uncinal teeth of unequal size above main fang; hood present. Three abdominal setigers.

REMARKS: *Augeneriella* is most closely related to *Fabricia*; both genera have the wide lobe state of the anterior peristomial ring and similar tooth arrangement over the main fang of thoracic uncini. The present diagnosis is similar to that given by Banse (1957) in distinguishing *Augeneriella* from other genera

by the presence of branched, vascularized ventral filamentous appendages.

Gitay (1970) later emended the diagnosis such that multiple or compound branching of ventral filamentous appendages was included. He also pointed out that *Augeneriella dubia* Hartmann-Schröder, 1965, differed from other species in the genus in that it (1) had teeth of equal size above the main fang, (2) did not have typical pseudospatulate setae, and (3) had unbranched, ventral filamentous appendages. Gitay therefore considered placement of *A. dubia* in this genus as questionable and did not recognize it in his emended diagnosis.

Hartmann-Schröder (1986) described the species, *Augeneriella bansei*, which has a pair of short, unbranched, ventral filamentous appendages. She suggested that the unbranched state be maintained as part of the generic diagnosis, substantiating inclusion of *A. dubia* in the genus. I have examined the holotype of *A. dubia* and found that it is a species within Genus A (see above).

The description of *Augeneriella bansei* was based on a single specimen and it is very likely that the nature of the ventral filamentous appendages in this specimen is abnormal. In *Augeneriella*, the structure of the ventral filamentous appendages appears to be size related. Examination of large numbers of specimens of the same species in various size classes has shown that in the smallest individuals the ventral filaments are unbranched (see also Banse, 1959; Gitay, 1970). As an individual grows, the ventral filaments begin to branch. Preliminary observations indicate that the pattern of branching and sequence of branch addition in ontogeny is species specific to some extent.

The recognition of species within *Augeneriella* in part depends on knowledge of the inherent variability associated with the ventral filamentous appendages. I would therefore consider *A. bansei*, described from a single, probably aberrant, specimen to be a member of *Augeneriella* and predict that branched ventral filamentous appendages will be found once more material becomes available. It is more appropriate to continue defining *Augeneriella* on the basis of branched, ventral filamentous appendages.

SABELLINAE JOHNSTON, 1846, REVISED

DIAGNOSIS: Small- to large-bodied sabellid genera; *radiolar skeleton with cells in two or more rows* (but see Remarks). Branchial lobes fused middorsally. Radiolar flanges common as well as dorsal and ventral radiolar appendages. Anterior peristomial ring with anterior margin as narrow, ventral lobe or may be modified as a wide lobe, or reduced to low, even segment. Posterior peristomial ring collar usually present. Postsetal glandular girdle sometimes present on setiger 2. Inferior thoracic notosetae usually present in the form of anterior and/or posterior groups, each comprising one or more rows each; rarely lost. Abdominal neurosetal fascicles composed of a single anterior and/or posterior row. Thoracic uncini variable, ranging from acicular to avicular. Abdominal uncini variable, as rasp-shaped plates or avicular.

REMARKS: The revised Sabellinae contains the largest number of sabellid genera and, as such, is the most heterogeneous with respect to transformation series. The above diagnosis is a barely adequate definition of this group; the only character consistently defining the Sabellinae is the nature of the radiolar skeleton, with at least two rows of cells. A possible exception to this condition has been reported by Knight-Jones (1983) in *Potamethus singularis* Hartman, in which there is only a single row of cells.

There is the possibility that the subfamily could also be defined by dorsal fusion of the branchial lobes. At this time, however, there is ambiguity as to how many times this state has been derived (fig. 28).

DESDEMONA BANSE, 1957

TYPE SPECIES: *Desdemona ornata* Banse, 1957, by monotypy.

DIAGNOSIS: Small-bodied sabellin species with three pairs of radioles; radiolar skeleton with two rows of cells. Palmate membrane absent; radiolar flanges present. Dorsal and ventral lips present; without dorsal radiolar or pinnular appendages. One pair of ventral radiolar appendages present. *Anterior margin of anterior peristomial ring developed ventrally as wide lobe*; posterior peristomial ring

collar absent. Glandular ridge on setiger 2, often obscure. Inferior thoracic notosetae are bayonet setae; situated as single row roughly parallel and posterior to superior notosetae. Abdominal neurosetae a single row of modified, elongate, narrowly hooded setae. Thoracic uncini acicular; teeth above main fang of equal size; hood absent. Abdominal uncini as rasp-shaped plates, without main fang; breast poorly developed; handles absent. Abdominal setigers number about eight.

REMARKS: *Desdemona* closely resembles *Oriopsis* in the type of abdominal uncini. The former differs in that a posterior peristomial ring collar is absent and the anterior peristomial ring lobe is wide ventrally instead of narrow. Also, the thoracic uncinal teeth of *Oriopsis* are of unequal size and a hood is present. Radiolar flanges were not mentioned by Banse (1957) but they were included in the diagnosis given by Day (1967).

The glandular ridge on setiger 2 is usually very indistinct even on large specimens and usually not visible on small individuals. This structure has not been reported for this genus and does not appear to be visible on the type material for the genus, although it is in poor condition. Larger specimens of *Desdemona ornata* from the type locality do, however, display the glandular ridge. Examination of the paratypes of *D. aniara* Hutchings and Murray, 1984, also demonstrated the presence of a girdle which was not noted in the original description.

ORIOPSIS CAULLERY AND MESNIL, 1896

TYPE SPECIES: *Oriopsis metchnikowi* Caullery and Mesnil, 1896, by monotypy.

DIAGNOSIS: Small-bodied sabellin species usually with 3–6 pairs of radioles; radiolar skeleton with two rows of cells. Palmate membrane and radiolar flanges present. Dorsal and ventral lips present; without dorsal radiolar or pinnular appendages. One or two pairs of ventral radiolar appendages present. Anterior margin of anterior peristomial ring developed ventrally as narrow lobe, distal end may be minutely bifid or trifid. Posterior peristomial ring collar present, usually of even height all around. Glandular ridge present on setiger 2, obscure on small individuals. In-

ferior thoracic notosetae are bayonet setae, situated as single row roughly parallel and posterior to superior notosetae. Abdominal neurosetae situated as single row of modified, elongate, narrowly hooded setae. Thoracic uncini acicular; teeth above main fang unequal in size; hood present. Abdominal uncini as rasp-shaped plates, without main fang; breast poorly developed; handles absent. Abdominal setigers usually number from four to 10.

REMARKS: Most recent workers have followed the diagnosis given by Banse (1957) for *Oriopsis*. This diagnosis was slightly modified by Knight-Jones (1983) in that it was acknowledged that a low palmate membrane is present; this view is continued here. It is, however, interesting to note that past definitions of *Oriopsis* have not been able to provide any synapomorphies for the genus. Based on the present results, the unequal size teeth above the main fang in thoracic uncini is the only synapomorphy capable of grouping species within this genus. This character is also homoplasious, occurring in most of the fabriciina genera.

In her diagnosis, Knight-Jones (1983) also stated that there is no dorsal fusion of the branchial lobes and that a skeleton is absent in this area. The branchial skeleton in the lobes of *Oriopsis* is present, although poorly developed, and is continuous through an area of middorsal fusion of the lobes. Also contrary to Knight-Jones' observation, ventral sacs are not present.

The glandular girdle on setiger 2 is present in most of the species examined, although often obscure. The girdle is usually not seen in very small individuals; it has only been reported once before, for *O. cincta*, by Hartmann-Schröder (1986).

In his discussion of the definitional problems related to *Chone*, Banse (1972: 461) made the statement that if the palmate membrane were to be considered a "specific character" in *Chone*, then difficulties would arise: "For example, a large species of *Oriopsis* . . . (cf. *O. rivularis* Annenkova, with bayonet-type thoracic notosetae) would externally be distinguishable from *Chone* only by the absence of the post-setal glandular girdle on the second setiger." I find it difficult to understand how *Oriopsis* could be confused with

Chone even if the palmate membrane is not taken into account. For instance, *Chone* is readily distinguished from *Oriopsis* since the former has two different groups of inferior thoracic notosetae, i.e., bayonet and paleate. In addition, the thoracic uncini of *Chone* have equal size teeth above the main fang.

CHONE KRÖYER, 1856

TYPE SPECIES: *Chone infundibuliformis* Kröyer, 1856, subsequent designation by Bush (1905).

DIAGNOSIS: Small- to large-bodied sabellin species with few to numerous radioles; radiolar skeleton with two rows of cells. Palmate membrane and radiolar flanges present. Dorsal lips present; with or without dorsal radiolar appendages. Ventral lips present. Ventral radiolar appendages present, numbering about two to eight pairs. Anterior margin of anterior peristomial ring with narrow, ventral lobe; posterior peristomial ring collar present. Glandular girdle on setiger 2. Inferior thoracic notosetae in two distinct, transverse groups: anterior row(s) of bayonet setae; posterior row(s) paleate. Abdominal neurosetae arranged in two transverse rows per fascicle: anterior row in anterior setigers with elongate, narrowly hooded setae; posterior row with modified, elongate, narrowly hooded setae; posterior abdominal fascicles with modified, elongate, narrowly hooded setae in both rows. Thoracic uncini acicular; teeth above main fang of equal size; hood present. Abdominal uncini usually with main fang surmounted by broad series of smaller teeth; breast well developed, expanded; handles absent. Regional variation in abdominal uncini may occur; anterior and posterior setigers with uncini of above form, or posterior setigers with rasp-shaped plates (*Oriopsis*-type). Abdominal setigers vary in number with size of individuals.

REMARKS: *Chone* most closely resembles *Euchone* in regard to general setal and posterior peristomial ring collar characters, as well as having a well-developed palmate membrane. *Chone* differs from *Euchone* in having paleate setae in the thorax, and *Euchone* has an anal depression, absent in *Chone*.

In his emendation of the diagnosis of *Chone*, Banse (1972) commented on the definitional problems with this genus, noting that Kröyer's (1856) original intent in erecting *Chone* was to indicate the distinct nature of the palmate membrane. Banse did not, however, suggest what characters might be used to define the genus, such that it is a monophyletic group.

In the present study, it was noted that some specimens identified as *Chone infundibuliformis* have dorsal lips which contain dorsal radiolar appendages (= *Chone*1), whereas other specimens do not (= *Chone*2). For the present study, it was found that *Chone*2 is plesiomorphic to *Chone*1 and *Euchone* on the basis of dorsal radiolar appendages being present in the two latter taxa.

Recently, Knight-Jones (1983) revised *Potamilla*, citing as a synapomorphy the absence of dorsal radiolar appendages. If the radiolar appendages have been lost in certain species of *Chone*, such a character could be of systematic use at the generic level. Exclusive of the apparent loss of the dorsal radiolar appendages in some species, *Chone* as a group is not defined by any synapomorphy. It is possible that species within *Chone*2 should be placed in a separate genus, defined by the loss of dorsal radiolar appendages. This, however, would leave all other species without any synapomorphy defining the genus. Before such a revision is made though, it will be necessary to reexamine all species in *Chone* and determine if lack of radiolar appendages is plesiomorphic or a secondary loss.

As with *Euchone*, a number of species of *Chone* display variation in abdominal uncinal form. Banse (1972) pointed out that when such variation occurred, uncini of the anterior region display a large main fang and well-developed breast whereas in the posterior region uncini more closely resemble those of *Oriopsis*. There is also the possibility of intrafascicular variation. It might be possible to divide the *Chone* complex into a series of monophyletic genera based on the presence or loss of dorsal radiolar appendages and abdominal uncinal variation. In the present analysis, intraabdominal uncinal variation was not taken into account since the type species displays a uniform uncinal form throughout the abdomen.

EUCHONE MALMGREN, 1866

TYPE SPECIES: *Sabella analis* Kröyer, 1856, subsequent designation by Bush (1905).

DIAGNOSIS: Small- to large-bodied sabellin species with three to many pairs of radioles. Radiolar skeleton with two rows of cells. Palmate membrane present in most species as well as radiolar flanges. Dorsal lips with dorsal radiolar appendages; ventral lips present. Ventral radiolar appendages present, ranging from about two to six pairs (number varies with size of individuals). Anterior margin of anterior peristomial ring ventrally as narrow lobe; posterior peristomial ring collar present. Glandular girdle present on setiger 2. Inferior thoracic notosetae as two transverse groups: anterior group (row or rows) of bayonet setae and *posterior row(s) of broadly hooded setae*. Abdominal neurosetae situated in two transverse rows per fascicle: anterior row in anterior setigers with elongate, narrowly hooded; posterior row in anterior setigers with modified, elongate, narrowly hooded; anterior and posterior setal rows in posterior setigers with only modified, elongate narrowly hooded setae. Thoracic uncini acicular; teeth above main fang of equal size; hood present. Anterior abdominal uncini with small teeth surmounting main fang; breast expanded, well developed; handles absent. Abdominal uncini in far posterior setigers, primarily in area of anal depression, may resemble rasp-shaped forms of *Oriopsis* or be transitional between these two forms. Abdominal setigers vary in number with size of individuals. *Anal depression extending anteriorly from pygidium through varying number of abdominal setigers.*

REMARKS: The above diagnosis agrees with that of Banse (1972) in most respects, although some additional characters are considered here.

Banse (1972) suggested that since the palmate membrane is absent in some species of *Euchone*, the presence of this character among genera should be considered a species-level phenomenon. Based on the above cladistic results, it is not appropriate to regard presence of the palmate membrane as a species-specific character among these two genera. Instead, the palmate membrane is a plesiomorphic character at both the generic and

specific level, being present not only in *Euchone* and *Chone*, but also *Oriopsis*, *Fabrisabella*, *Myxicola*, etc. Loss of the palmate membrane in some species of *Euchone* can be regarded simply as a possible autapomorphic condition at the subgeneric or specific level.

As noted by Banse (1970, 1972), the shape of abdominal uncini may be variable especially with respect to location within a fascicle or a given region in the abdomen. In the present analysis, only adult specimens of the type species were considered in this regard and uncinal variation does not occur in *Euchone analis*. Further work is needed to understand the relationship of uncinal differences within and among fascicles to ontogeny and systematics within this genus.

Both *Euchone* and *Chone* display great interspecific size variability. In the present study, no attempt was made, for example, to determine consistency of abdominal neurosetal distribution patterns in relation to size differences, or degree of ventral shield development. Since these attributes have not been investigated extensively, future revisionary work will be needed to determine to what extent such variation can be included in generic diagnoses.

JASMINEIRA LANGERHANS, 1880

TYPE SPECIES: *Jasmineira caudata* Langerhans, 1880, by monotypy.

DIAGNOSIS: Small- to medium-size sabellin species with few to numerous pairs of radioles; radiolar skeleton with two rows of cells. Palmate membrane absent; radiolar flanges present. Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages absent. Ventral lips and parallel lamellae present. Ventral radiolar appendages present (few to many pairs). Anterior margin of anterior peristomial ring with narrow, ventral lobe; posterior peristomial ring collar present. Glandular ridge on setiger 2. Inferior thoracic notosetae in form of two transverse rows or groups: anterior row(s) of bayonet setae, posterior row(s) as paleate setae. Abdominal neurosetal fascicles arranged in two transverse rows: anterior row in anterior setigers with elongate, narrowly hooded setae; posterior row in anterior setigers with modified,

elongate, narrowly hooded setae; anterior and posterior rows in posterior setigers with modified, elongate, narrowly hooded setae. Thoracic uncini acicular; teeth above main fang of equal size; hood present. Abdominal uncini with main fang surmounted by series of equal size teeth; *breast reduced to narrow swelling*; handles long. Abdominal setigers number several to many, depending on size of individuals.

REMARKS: Most diagnoses of *Jasmineira* have concentrated on the fact that thoracic acicular uncini are present in combination with what have been referred to as abdominal avicular uncini. It is more descriptive to specifically regard abdominal uncini as having a narrow or reduced breast, a condition which is not implicit in the term avicular.

While combinations of some characters can distinguish *Jasmineira* from other genera, they do not constitute synapomorphies. The loose association of characters which have in the past described, but not necessarily defined, *Jasmineira* need to be examined in all presently recognized species to insure consistency. At this time, the only character which establishes the monophyly of *Jasmineira* in the cladograms generated is reduction of the abdominal uncinal breast to a narrow swelling, which also arises independently in *Fabrisabella*, *Potamethus*, and *Potaspina*.

Most of the transformation series for the handles of abdominal uncini allow for independent derivation of the long-handled state in *Jasmineira*. Unique derivations of the handle are, however, only possible for cladograms with areas IIa and IIc, d (figs. 28, 29).

PANOUSEA RULLIER AND AMOUREUX, 1970

TYPE SPECIES: *Panousea africana* Rullier and Amoureux, 1970, by monotypy.

DIAGNOSIS: Medium-size sabellin species with numerous radioles; radiolar skeleton with two rows of cells. Palmate membrane and *radiolar flanges absent*. Dorsal lips present, with dorsal radiolar appendages; *single dorsal pinnular appendage fused with dorsal margin of each dorsal lip*. Ventral lips and parallel lamellae present. Several ventral radiolar appendages present. Anterior margin

of anterior peristomial ring with narrow, ventral lobe; posterior peristomial ring collar present. Glandular girdle on setiger 2. *Collar setae fascicle (setiger 1) arranged as elongate row, oriented at an angle slightly divergent from long axis of body*. *Collar setae short, spinelike*. Inferior thoracic notosetae arranged in two transverse groups: anterior row of bayonet setae; two posterior rows of paleate setae. Abdominal neurosetal fascicles arranged in two transverse rows: anterior row in anterior setigers elongate, narrowly hooded setae; posterior row in anterior setigers modified, elongate, narrowly hooded setae; anterior and posterior rows in posterior setigers modified, elongate, narrowly hooded setae. Thoracic uncini acicular; teeth above main fang of equal size; hood present. *Companion setae with distal membranous end roughly symmetrical, teardrop-shaped*. Abdominal uncini with main fang surmounted by series of smaller teeth; breast well developed, expanded; handles absent. Abdominal setigers numerous.

REMARKS: *Panousea* is an unusual genus in that it has companion setae similar to those of the more apomorphic sabellins and collar setae similar to and arranged in the manner seen in *Notaulax*. The cladistic analysis indicates that *Panousea* acquired these states independently of other sabellin taxa. Setal forms in remaining thoracic and abdominal setigers resemble those seen in *Chone* and *Jasmineira*. An additional synapomorphy is loss of radiolar flanges. Depending on the transformation series, the lack of abdominal uncinal handles may be plesiomorphic or a secondary loss (fig. 28).

The description given by Rullier and Amoureux (1970) overlooked a number of important characters. For instance, the elongate arrangement of the setiger 1 fascicles was not mentioned and the figure of the anterior end does not accurately show this feature. The setae of setiger 1 were referred to only as "limbate"; the marked difference between the collar setae and the superior notosetae of remaining thoracic notopodia was not described. The glandular girdle, as well as the presence of bayonet setae, was not noted. Had these characters been included, the authors probably would not have considered *Panousea* as being most similar to *Potamilla*. The

diagnosis given by Fauchald (1977) only referred to thoracic uncini as "long-handled"; the narrowed breast common to acicular uncini was not mentioned.

FABRISABELLA HARTMAN, 1969

TYPE SPECIES: *Fabrisabella vasculosa* Hartman, 1969, by monotypy.

DIAGNOSIS: Medium-size sabellin species with numerous pairs of radioles; radiolar skeleton with two rows of cells. Palmate membrane and radiolar flanges present. Dorsal lips present, *dorsal radiolar appendages absent*; pinnular appendages absent. Ventral lips present; parallel lamellae absent. Ventral radiolar appendages present. Anterior margin of anterior peristomial ring with narrow, ventral lobe; posterior peristomial ring collar present. *Two pairs of distinct vascular coils visible dorsally below collar*. Glandular girdle on setiger 2. Inferior thoracic notosetae single group of paleate setae arranged in two or more transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior row in anterior abdominal setigers composed of elongate, narrowly hooded setae; posterior row with modified, elongate, narrowly hooded setae; anterior and posterior rows in posterior setigers with modified, elongate, narrowly hooded setae. Thoracic uncini acicular; teeth above main fang equal in size; hood present. Abdominal uncini with main fang surmounted by teeth of equal size; *breast reduced to narrow swelling*; handles long. Abdominal setigers numerous.

REMARKS: Hartman (1969) considered *Fabrisabella* distinct in that it has what she interpreted to be "subavicular" thoracic uncini. Based on examination of the paratype material, the thoracic uncini do not appear fundamentally different from typical thoracic acicular uncini. To what degree the presence of distinct anterior vascular loops can be considered a synapomorphy is still questionable (L. Harris, personal commun.).

It is likely that *Fabrisabella* is often confused with *Jasmineira* since both have acicular thoracic uncini and abdominal uncini with a reduced, narrow breast and long handle. It is possible to hypothesize derivation of the handle as an autapomorphy or as a more plesiomorphic condition in all cladograms gen-

erated. Loss of dorsal radiolar appendages and bayonet setae can also distinguish *Fabrisabella* from *Jasmineira*.

MYXICOLA KOCH IN RENIER, 1847

TYPE SPECIES: *Terebella infundibulum* Renier, 1804, subsequent designation by Bush (1905).

DIAGNOSIS: Medium- to large-size sabellin species with numerous radioles; radiolar skeleton with two rows of cells. Palmate membrane and radiolar flanges present. *Dorsal lips as thickened outgrowths; distinctly curved into cuplike shape. Dorsal radiolar appendages not fused with lips but emerging medially from lip base on margin opposite branchial lobes* (surrounded in part by dorsal lips). *Ventral lips absent*. Ventral radiolar appendages usually three to six pairs. Margin of anterior peristomial ring modified ventrally as narrow lobe; *posterior peristomial ring collar absent*. Glandular girdle present on setiger 2. *Thoracic notosetal fascicles arranged in irregular bundles; superior and inferior setal groups not distinct (each bundle assumed to represent only superior group)*. Abdominal neurosetal fascicles similar to those of thoracic notosetal fascicles; *setae in this group assumed to be from anterior setal row(s)*. *Thoracic notopodial and abdominal neuropodial tori developed as low, circular elevations*. Thoracic uncini acicular; teeth above main fang of equal size; hood absent. Abdominal uncini with main fang surmounted by series of smaller teeth; breast well developed, expanded; handles absent. *Abdominal uncini distributed on narrow tori which form almost complete cinctures around each setiger*. Abdominal setigers numerous.

REMARKS: Past definitions of *Myxicola* have restricted attention only to the high palmate membrane and have regarded the nature of abdominal uncinigerous tori as important. Extent of development of the palmate membrane is a rather dubious character on which to define a genus considering the variable development of the membrane in species of other genera. Meyer (1888) did note the absence (or loss) of ventral lips, but this condition has never been used as a systematic character. As can be seen from the present diagnosis, *Myxicola* is readily defined by a

number of states not usually considered in the past.

POTAMETHUS CHAMBERLIN, 1919

TYPE SPECIES: *Potamis spathiferus* Ehlers, 1887, by monotypy.

DIAGNOSIS: Medium-size sabellin species with numerous pairs of radioles; radiolar skeleton usually with four or more rows of cells. Palmate membrane present; radiolar flanges absent. Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages absent. Ventral lips and parallel lamellae present. Ventral radiolar appendages absent. Anterior margin of anterior peristomial ring with narrow, ventral lobe; posterior peristomial ring collar present. *Posterior peristomial ring distinctly elongate, often extending anteriorly beyond collar.* Glandular girdle on setiger 2. Inferior thoracic notosetae two or more transverse rows of paleate setae. Abdominal neuropodia with setal fascicles in two rows: anterior row in anterior and posterior setigers with elongate, narrowly hooded setae; posterior row in same setigers with modified, elongate, narrowly hooded setae. Thoracic uncini avicular; teeth above main fang of equal size; hood absent; breast may be well developed and expanded, or narrower, verging on acicular condition; long handled. Companion setae with roughly symmetrical, teardrop-shaped distal membranes. Abdominal uncini with main fang surmounted by series of equal size teeth; *breast reduced to narrow swelling*; long handled. Abdominal setigers numerous.

REMARKS: The above diagnosis agrees for the most part with that given by Knight-Jones (1983) except that the presence of ventral sacs is not included since this character is inconsistently present in a number of genera (see above). A palmate membrane is also considered present, which Knight-Jones stated is absent. Of the specimens examined, there appears to be a very low membrane.

The present diagnosis also states that the radiolar skeleton usually has four or more rows of cells. Knight-Jones (1983) stated, however, that *Potamethus singularis* Hartman has only a single row of cells.

The principal synapomorphies defining *Potamethus* are the narrow breast of abdom-

inal uncini (see Remarks for *Jasmineira*) and the elongate posterior peristomial ring.

In the cladistic analysis, states for thoracic uncini in *Potamethus* suggest that the general uncinal shape in this genus is transitional between typical acicular and avicular forms (see discussion below). This conclusion was, however, based on data from species which have a well-developed breast, which does not appear to be the case throughout the genus (e.g., Knight-Jones, 1983). Further work at the specific level should establish whether the expanded breast is plesiomorphic for *Potamethus*.

SABELLA LINNAEUS, 1767

TYPE SPECIES: *Sabella pavonina* Savigny, 1822, subsequent designation by Bush (1905).

DIAGNOSIS: Medium- to large-size sabellin species with numerous pairs of radioles; radiolar skeleton with four or more rows of cells. *Outer margin of radioles rounded in cross section.* Palmate membrane present; radiolar flanges absent. Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages absent. Ventral lips and parallel lamellae present. Anterior margin of anterior peristomial ring with narrow, ventral lobe; posterior peristomial ring collar present. Interramal eyespots present in thoracic and abdominal setigers. Inferior thoracic notosetal fascicles arranged in bundles, with irregular, longitudinal setal rows. Inferior thoracic notosetae spinelike. Abdominal neurosetal tori as conical lobes; *neurosetal fascicles in tight spiral formation.* Anterior abdominal neuropodial fascicles with only anterior setal row, composed of spinelike setae, posterior row absent; *posterior fascicles with anterior row of spinelike setae; modified, elongate, narrowly hooded setae in center of spiral.* Thoracic uncini avicular; teeth above main fang of equal size; hood absent; breast well developed, expanded; medium-length handles. Companion setae with distal ends as distinctly asymmetrical membranes. Abdominal uncini with main fang surmounted by teeth of equal size; breast well developed, expanded; long handled. Abdominal setigers numerous.

REMARKS: The revisionary work of Perkins and Knight-Jones (in press) on *Sabella* has contributed a great deal toward defining this

genus better. *Sabella* is similar in general appearance to *Bispira* in that both have companion setae with a distinctly asymmetrical distal end. *Sabella*, however, lacks compound eyes on the radioles. *Sabella* is well defined in having abdominal neurosetae arranged in a very tight spiral pattern.

BISPIRA KRÖYER, 1856

TYPE SPECIES: *Amphitrite voluticornis* Montagu, 1804, subsequent designation by Claparède (1870).

DIAGNOSIS: Medium- to large-size sabellin species with numerous pairs of radioles; radiolar skeleton with four or more rows of cells. Palmate membrane and radiolar flanges present. Radiolar eyes compound, paired, distributed along radiolar length. Dorsal lips with radiolar appendages; pinnular appendages present. Ventral lips and parallel lamellae present. Anterior margin of anterior peristomial ring with narrow, ventral lobe; posterior peristomial ring collar present. Thoracic and abdominal interramal eyespots present. Inferior thoracic notosetal fascicles arranged in bundles, with irregular, longitudinal setal rows. Inferior thoracic notosetae spinelike. Abdominal neurosetal tori as conical lobes. Abdominal neurosetal fascicles arranged in partial spiral or C-shaped configuration, formed by anterior setal row; original posterior setal row as small bundle partially enclosed by anterior row. Anterior abdominal neurosetae spinelike in anterior and posterior rows; posterior abdominal neurosetae spinelike in anterior rows, and modified, elongate, narrowly hooded in posterior rows. Thoracic uncini avicular; teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends as distinctly asymmetrical membranes. Abdominal uncini with main fang surmounted by teeth of equal size; breast well developed, expanded; long handled. Abdominal setigers numerous.

REMARKS: *Bispira* is similar to *Sabella* in the shape of companion setae. While *Bispira* and *Branchiomma* appear similar with respect to the occurrence of compound eyes over the length of the radioles, the present analysis indicates that this character state has been independently derived. These two gen-

era differ in that companion setae are absent in *Branchiomma*.

It is important to note that *Bispira* is also defined in the present study by the independent acquisition of radiolar flanges and dorsal pinnular appendages. The occurrence of spinelike setae in the posterior rows of anterior abdominal neurosetal fascicles is considered a synapomorphy in some transformation series (discussed below; see fig. 34), whereas in others, this state is plesiomorphic for the *Sabella-Bispira* clade.

SABELLASTARTE KRÖYER, 1856

TYPE SPECIES: *Sabellastarte indica* Savigny, 1822, subsequent designation by Bush (1905).

DIAGNOSIS: Large-bodied sabellin species with numerous radioles; radiolar skeleton with four or more rows of cells. Palmate membrane present; radiolar flanges absent. Dorsal lips with dorsal radiolar appendages. Ventral lips present, with parallel lamellae. Anterior margin of anterior peristomial ring with narrow, ventral lobe; posterior peristomial ring collar present. Thoracic and abdominal interramal eyespots present. Inferior thoracic notosetal fascicles arranged in bundles with irregular, longitudinal setal rows. Inferior thoracic notosetae spinelike. Abdominal neurosetal tori conical lobes. Abdominal neurosetal fascicles arranged in partial spiral or C-shaped configuration, formed by anterior setal row; original posterior setal row as small bundle partially enclosed by anterior row. Anterior abdominal neurosetae spinelike in anterior rows; elongate, narrowly hooded in posterior rows; posterior abdominal neurosetae spinelike in anterior rows; modified, elongate, narrowly hooded in posterior rows. Thoracic uncini avicular; teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. Companion setae absent. Abdominal uncini with main fang surmounted by teeth of equal size; breast well developed, expanded; long handled. Abdominal setigers numerous.

REMARKS: *Sabellastarte* does not appear to be a definable genus based on the characters examined. In the past, *Sabella* (including *Spirographis*), *Bispira*, and *Sabellastarte* have been defined in part by the degree of bran-

chial crown spiraling. The fact that such a character is not applicable at the generic level (see Perkins, 1984; Perkins and Knight-Jones, in press) has only been recognized recently. The impact that this could have on the generic groupings within the clade with spine-like setae is not yet known.

Relationships among members in the clade with inferior spinelike thoracic notosetae will be better understood with the revisions being undertaken by Perkins and Knight-Jones (in press). At this level, such features as the ventral shields appear to be very informative systematically (T. H. Perkins, personal commun.).

PSEUDOBANCHIOMMA JONES, 1962

TYPE SPECIES: *Pseudobranchiomma emersoni* Jones, 1962, by monotypy.

DIAGNOSIS: Medium-size sabellin species with numerous pairs of radioles; radiolar skeleton with four or more rows of cells. Palmate membrane and *radiolar flanges present*. Stylodes present, poorly developed as low, rounded elevations. Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages absent. Ventral lips and parallel lamellae present. Anterior margin of anterior peristomial ring with narrow, ventral lobe; posterior peristomial ring collar present. Thoracic and abdominal interrampal eyespots present. Inferior thoracic notosetal fascicles arranged in bundles, with irregular, longitudinal setal rows. Inferior thoracic notosetae spinelike. Abdominal neurosetal tori conical lobes. Abdominal neurosetal fascicles arranged in partial spiral or C-shaped configuration, formed by anterior setal row; original posterior setal row a small bundle partially enclosed by anterior row. Anterior and *posterior setal rows* of all abdominal fascicles composed of spinelike and *modified, elongate, narrowly hooded setae*, respectively. Thoracic uncini avicular; teeth above main fang of equal size; hood absent; breast well developed, expanded; handles very short. Companion setae absent. Abdominal uncini with main fang surmounted by teeth of equal size; breast well developed, expanded; handles very short. Abdominal setigers numerous.

REMARKS: *Pseudobranchiomma* most

closely resembles *Branchiomma* in the occurrence of stylodes on the outer margins of the radioles. *Pseudobranchiomma*, however, differs in that the stylodes are poorly developed and radiolar compound eyes are lacking. *Pseudobranchiomma* is also defined by the occurrence (as a reversal) of modified, elongate, narrowly hooded setae in the posterior setal rows of anterior abdominal neuropodia.

The number of thoracic setigers (totaling four) is not included as a diagnostic feature (fide Jones, 1962) since this meristic character needs to be examined in the entire sabellid group. Furthermore, reduced stylodes may not be an autapomorphy for *Pseudobranchiomma* (e.g., fig. 28), hence they have not been designated as such in the present diagnosis.

Jones (1962) pointed out that some species of *Branchiomma* display a lappet condition similar to that in *Pseudobranchiomma* and also lack radiolar eyes. A complete revision of *Branchiomma*, however, might either entail (1) moving some of these species into *Pseudobranchiomma* irrespective of number of thoracic setigers, or (2) placing *P. emersoni* into *Branchiomma*, with the general presence of stylodes as a synapomorphy.

BRANCHIOMMA KÖLLIKER, 1858

TYPE SPECIES: *Amphitrite bombyx* Dalyell, 1853 (= *Branchiomma dalyelli* Kölliker), by monotypy.

DIAGNOSIS: Medium-size sabellin species with numerous radioles; radiolar skeleton with four or more rows of cells. Palmate membrane present; radiolar flanges absent. Stylodes present, well developed. *Radiolar compound eyes present, paired, distributed along length of radioles*. Dorsal lips with radiolar appendages; *dorsal pinnular appendages present*. Ventral lips and parallel lamellae present. Anterior margin of anterior peristomial ring with narrow, ventral lobe; posterior peristomial ring collar present. Thoracic and abdominal interrampal eyespots present. Inferior thoracic notosetal fascicles arranged in bundles, with irregular, longitudinal setal rows. Inferior thoracic notosetae spinelike. Abdominal neurosetal tori conical lobes. Abdominal neurosetal fascicles ar-

ranged in a partial spiral or C-shaped configuration, formed by anterior setal row; original posterior setal row a small bundle partially enclosed by anterior row. Anterior abdominal neurosetae spinelike in anterior rows and elongate, narrowly hooded in posterior rows; posterior abdominal neurosetae spinelike in anterior rows and modified, elongate, narrowly hooded in posterior rows. Thoracic uncini avicular; teeth above main fang of equal size; hood absent; breast well developed, expanded; handles very short. Companion setae absent. Abdominal uncini with teeth of equal size surmounting main fang; breast well developed, expanded; handles very short. Abdominal setigers numerous.

REMARKS: The above diagnosis is more restrictive than those of the past in that only forms with well-developed stylodes are included. The present analysis hypothesizes that radiolar compound eyes of *Bispira* and *Branchiomma* are independently derived, as well as dorsal pinnular appendages. As noted in the remarks on *Pseudobranchiomma*, the current diagnosis may force the transfer of some species from *Branchiomma* to *Pseudobranchiomma* when the former is revised. All of the cladograms present the possibility of well-developed stylodes being a synapomorphy for *Branchiomma*, but this is still uncertain (fig. 28).

ANAMOBAEA KRÖYER, 1856

TYPE SPECIES: *Anamobaea orstedii* Krøyer, 1856, by monotypy.

DIAGNOSIS: Medium-size sabellin species with numerous radioles; radiolar skeleton with four or more rows of cells. Palmate membrane present; radiolar flanges absent. Simple radiolar eyespots present in narrow band above palmate membrane. Dorsal lips with dorsal radiolar appendages; *dorsal pinnular appendages present*. Ventral lips and parallel lamellae present. *Two pairs of erect flanges* (= *branchial crown*, *ventral basal flanges*; broad flanges sensu Perkins 1984), *each pair situated dorsally and ventrally, respectively; originate on branchial lobes and extend posteriorly, terminating on posterior peristomial ring*. Anterior margin of anterior peristomial ring low, of even height all around; posterior peristomial ring collar present.

Thoracic setigers very numerous (>50). Inferior thoracic notosetae paleate, arranged in two transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae; anterior and *posterior rows* in all setigers paleate setae and *modified, elongate, narrowly hooded setae*, respectively. Thoracic uncini avicular; teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends as roughly symmetrical, teardrop-shaped membranes. Abdominal uncini with teeth above main fang of equal size; breast well developed, expanded; long handled. Abdominal setigers numerous.

REMARKS: *Anamobaea* is monotypic and was placed into synonymy with *Hypsicomus* by Augener (1925; see also Hartman, 1959). In his revision of *Hypsicomus* and *Notaulax*, Perkins (1984) recognized *Anamobaea*, stating that *A. orstedii* has dorsal and ventral branchial crown basal flanges, not present on *Hypsicomus*; Perkins also noted that *Hypsicomus* has two pairs of "accessory lamellae" (see below) not found in *Anamobaea*.

Like *Pseudobranchiomma*, *Anamobaea* is defined, in part, by reversal of the setal state in posterior setal rows of anterior abdominal neuropodia to modified, elongate, narrowly hooded.

HYPsicOMUS GRUBE, 1870

TYPE SPECIES: *Sabella stichophthalmos* Grube, 1863, subsequent designation by Bush (1905).

DIAGNOSIS: Medium-size sabellin species with numerous radioles; radiolar skeleton with four or more rows of cells. Palmate membrane and radiolar flanges present. Simple radiolar eyespots present in narrow band above palmate membrane. Dorsal lips with dorsal radiolar appendages; *dorsal pinnular appendages absent*. Ventral lips present, with parallel lamellae. Anterior margin of anterior peristomial ring low, of even height all around. Posterior peristomial ring collar present; posterior peristomial ring elongate, extending well beyond collar. *Two pairs of accessory lamellae* (sensu Perkins, 1984); dorsal pair originating dorsolaterally, slightly curved, rounded distally; ventral pair collarlike, originating slightly anterior to dorsal pair, ex-

tending ventrally to near ventral midline, partially obscuring ventral sacs; may be covered by ventral margins of collar. Inferior thoracic notosetae paleate, arranged in two transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior rows in all abdominal setigers with paleate setae; posterior row in anterior abdominal setigers with elongate, narrowly hooded setae; posterior row in posterior abdominal setigers with modified, elongate, narrowly hooded setae. Thoracic uncini avicular; teeth above main fang equal in size; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends as roughly symmetrical, teardrop-shaped membranes. Abdominal uncini with main fang surmounted by teeth of equal size; breast well developed, expanded; handles long. Abdominal setigers numerous.

REMARKS: Perkins (1984) revised *Hypsicomus*, noting that most of the described species do not belong in this genus. *Hypsicomus* has been defined in the past by the occurrence of an elongate notosetal fascicle in setiger 1, similar to that seen in *Panousea*. Since the type species, *H. stichophthalmos*, displays collar setae in a typical short bundle or arc, Perkins (1984) moved most species of *Hypsicomus* to *Notaulax*.

Hypsicomus is similar to *Anamobaea* in having an elongate posterior peristomial ring as well as simple radiolar eyespots and abdominal paleae. The two genera differ in that *Hypsicomus* has two pairs of accessory lamellae, whereas the posterior peristomial ring of *Anamobaea* has distinct dorsal and ventral flanges. Also, radiolar flanges are present in *Hypsicomus* as well as elongate, narrowly hooded setae in anterior abdominal setigers.

NOTAULAX TAUBER, 1879

TYPE SPECIES: *Notaulax* n. sp. Tauber, 1879 = *N. rectangulata* Levinsen, 1883, by monotypy.

DIAGNOSIS: Medium- to large-size sabellin species with numerous radioles; radiolar skeleton with four or more rows of cells. Palmate membrane and radiolar flanges present. Simple radiolar eyes present above palmate membrane. Dorsal lips present, with dorsal

radiolar appendages; dorsal pinnular appendages absent. Ventral lips and parallel lamellae present. *Branchial lobes very long* (basal lamina sensu Perkins, 1984); *dorsal and ventral margins with flanges* (basal flanges sensu Perkins, 1984) *which extend from base of lobes to origins of dorsalmost and ventralmost radioles*. Anterior margin of anterior peristomial ring low, of even height all around; posterior peristomial ring collar present. *Collar setae fascicles modified as single, elongate row of spinelike setae; fascicles longitudinal to oblique*. *Superior notosetae of setigers 2–8 spinelike*. Inferior thoracic notosetae paleate, arranged in two transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior row in anterior and posterior abdominal setigers paleate; posterior row in anterior abdominal setigers elongate, narrowly hooded; posterior row in posterior abdominal setigers modified, elongate, narrowly hooded. Thoracic uncini avicular; teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends as roughly symmetrical, teardrop-shaped membranes. Abdominal uncini with teeth of equal size surmounting main fang; breast well developed, expanded; long handled. Abdominal setigers numerous.

REMARKS: The above diagnosis follows that of Perkins (1984), who revised the genus to contain species with abdominal paleate setae and elongate collar segment (setiger 1) fascicles.

Notaulax resembles *Hypsicomus* and *Anamobaea* in the occurrence of simple radiolar eyes and abdominal paleate setae. The genus is distinctive in the arrangement of collar setae, presence of superior thoracic spinelike notosetae, and the long branchial base flanges.

DEMONAX Kinberg, 1867

TYPE SPECIES: *Demonax krusensterni* Kinberg, 1867, subsequent designation by Bush (1905).

DIAGNOSIS: Medium- to large-size sabellin species with numerous radioles; radiolar skeleton with four or more rows of cells. Palmate membrane and radiolar flanges absent. Dorsal lips with dorsal radiolar appendages and 1–3 dorsal pinnular appendages. Ventral

lips and parallel lamellae present. Anterior margin of anterior peristomial ring low, even height all around; posterior peristomial ring collar present. Inferior thoracic notosetae broadly hooded, arranged in several transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior and posterior setal rows in anterior abdominal setigers with elongate, narrowly hooded setae; anterior rows in posterior abdominal setigers with elongate, narrowly hooded setae; posterior rows in posterior abdominal setigers with modified, elongate, narrowly hooded setae. Thoracic uncini avicular; teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. *Companion setae with distal ends slightly inflated, dentate; thin membrane or mucro extending from dentate area.* Abdominal uncini with main fang surmounted by teeth of equal size; breast well developed, expanded; long handled. Abdominal setigers numerous.

REMARKS: The revised diagnosis given by Perkins (1984) is, for the most part, followed here. Perkins noted that past definitions of *Demonax* have been based on the presence of spiraled radioles or the near-paleate, or subspatulate, condition of inferior thoracic notosetae, or both. As has been pointed out by Perkins (1984), and Perkins and Knight-Jones (in press) for *Sabella* and *Bispira*, the spiraled condition is not a consistent character at the generic level in this instance. The primary character distinguishing *Demonax* is the distal dentate condition of companion setae.

Demonax most closely resembles *Megalomma* in having broadly hooded inferior thoracic notosetae and a similar arrangement of abdominal neurosetae. The two genera differ in the types of companion setae present and the fact that *Megalomma* has radiolar compound eyes which are limited to the distal ends of some (two or most) radioles.

MEGALOMMA JOHANSSON, 1927

TYPE SPECIES: *Amphitrite vesiculosum* Montagu, 1815, subsequent designation by Hartman (1959).

DIAGNOSIS: Medium- to large-size sabellin species with numerous radioles; radiolar

skeleton with four or more rows of cells. Palmate membrane and radiolar flanges absent. *One or more pairs of compound eyes present; one per radiole, each located on inner margin of radiole near distal end.* Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages present. Ventral lips and parallel lamellae present. Anterior margin of anterior peristomial ring low, even height all around; posterior peristomial ring collar present. Inferior thoracic notosetae broadly hooded, arranged in two or more transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior and posterior rows in anterior setigers with elongate, narrowly hooded setae; anterior and posterior rows in posterior setigers with elongate, narrowly hooded and modified, elongate, narrowly hooded setae, respectively. Thoracic uncini avicular; teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends as roughly symmetrical, teardrop-shaped membranes. Abdominal uncini with main fang surmounted by teeth of equal size; breast well developed; long handled. Abdominal setigers numerous.

REMARKS: The above diagnosis basically follows that given by Perkins (1984).

LAONOME MALMGREN, 1866

TYPE SPECIES: *Laonome kroyeri* Malmgren, 1866, by monotypy.

DIAGNOSIS: Medium-size sabellin species with numerous radioles; radiolar skeleton with two rows of cells. Palmate membrane and radiolar flanges absent. Dorsal lips present; *dorsal radiolar appendages absent*; dorsal pinnular appendages absent. Ventral lips present, parallel lamellae absent. *Anterior margin of anterior peristomial ring modified with narrow ventral lobe*; posterior peristomial ring collar present. Inferior thoracic notosetae paleate, arranged in two or more transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior and posterior rows in anterior setigers with elongate, broadly hooded setae; anterior and posterior rows in posterior setigers with elongate, broadly hooded and modified, elongate, narrowly hooded setae, respectively.

Thoracic uncini with teeth above main fang of equal size; hood absent; breast well developed, expanded; *handles absent*. Companion setae absent. Abdominal uncini with main fang surmounted by teeth of equal size; breast well developed, expanded; handles absent. Abdominal setigers numerous.

REMARKS: *Laonome* is distinguished by the lack of companion setae and the absence of handles on thoracic and abdominal uncini. Uncini from both regions of the body are similar in appearance and resemble the abdominal uncini of some *Chone* species (e.g., *C. infundibuliformis*).

With respect to features actually defining *Laonome*, only the loss of dorsal radiolar appendages, modification of the anterior peristomial ring, and loss of thoracic uncinal handles can be considered synapomorphies. Depending on the transformation series examined, the lack of companion setae and abdominal uncinal handles may also be synapomorphies. In other instances, these features define the *Laonome-Amphiglena* clade.

Laonome resembles *Potamilla* to some extent in that both have lost dorsal radiolar appendages and have elongate, broadly hooded setae in abdominal neuropodia. *Potamilla*, however, has both a palmate membrane and companion setae.

AMPHIGLENA CLAPARÈDE, 1864

TYPE SPECIES: *Amphicora mediterranea* Leydig, 1851, subsequent designation by Bush (1905).

DIAGNOSIS: Small-size sabellin species with 6–8 pairs of radioles; radiolar skeleton with two rows of cells. Palmate membrane and radiolar flanges absent. Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages absent. *Ventral lips absent*; parallel lamellae absent. *Paired, ventral basal flanges of branchial crown present, extending from posterior peristomial ring to proximal region of ventralmost radioles of both branchial lobes*. Anterior margin of anterior peristomial ring low, of even height all around. *Posterior peristomial ring collar absent*. *Superior thoracic notosetae broadly hooded*. Inferior thoracic notosetae paleate, arranged in single transverse row. Abdominal neurosetal fascicles

with only a single transverse row of setae, assumed to be anterior row (*posterior row absent*); composed of elongate, broadly hooded setae. Thoracic uncini with teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends slightly inflated, dentate; thin membrane or mucro extending from dentate ends. Abdominal uncini with main fang surmounted by teeth of equal size; breast well developed, expanded; handles very short. Abdominal setigers not numerous.

REMARKS: Several of the characteristics of *Amphiglena* are probably correlated, in part, with its small size, i.e., loss of ventral lips, only two rows of radiolar skeletal cells, and loss of the collar. The companion setae have only been vaguely described in the past. Based on the present analysis, the dentate condition seen in *Amphiglena* is derived independently from that seen in *Demonax*. There is ambiguity as to whether presence of this type of companion setae is a synapomorphy for the genus since there are a large number of possible transformation series. A similar problem arises in relation to the length of handles in abdominal uncini (fig. 28).

POTAMILLA MALMGREN, 1866

TYPE SPECIES: *Sabella neglecta* Sars, 1850, subsequent designation by Bush (1905).

DIAGNOSIS: Medium-size sabellin species with numerous radioles; radiolar skeleton with four or more rows of cells. *Palmate membrane present*; radiolar flanges absent. *Dorsal lips without dorsal radiolar appendages*; dorsal pinnular appendages present. Ventral lips and parallel lamellae present. Anterior margin of anterior peristomial ring low, of even height all around; posterior peristomial ring collar present. Inferior thoracic notosetae paleate, arranged in two or more transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae; both rows composed of elongate, broadly hooded setae in all setigers. Thoracic uncini with teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends as roughly symmetrical, teardrop-shaped membranes. Abdominal uncini with teeth

above main fang of equal size; breast well developed, expanded; long handled. Abdominal setigers numerous.

REMARKS: The above diagnosis differs only slightly from the revised definition given by Knight-Jones (1983). *Potamilla* is a member of the clade which contains genera such as *Perkinsiana*, *Pseudopotamilla*, and *Eudistylia*, all of which have elongate, broadly hooded abdominal neurosetae. Except for *Potamilla*, all of these genera have dorsal radiolar appendages, but lack a palmate membrane. Based on the above cladistic results, the palmate membrane in *Potamilla* has been independently derived.

PERKINSIANA KNIGHT-JONES, 1983

TYPE SPECIES: *Sabella rubra* Langerhans, 1880, by original designation.

DIAGNOSIS: Small- to medium-size sabellin species with numerous radioles; radiolar skeleton with four or more rows of cells. Palmate membrane and radiolar flanges absent. Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages present. Ventral lips and parallel lamellae present. Anterior margin of anterior peristomial ring low, of even height all around; posterior peristomial ring collar present. Inferior thoracic notosetae paleate, arranged in two or more transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior and posterior rows with elongate, broadly hooded setae in all setigers. Thoracic uncini with teeth of equal size above main fang; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends as roughly symmetrical, teardrop-shaped membranes. Abdominal uncini with equal-size teeth above main fang; breast well developed, expanded; long handled. Abdominal setigers numerous.

REMARKS: In her examination of species usually assigned to the genera *Demonax*, *Potamilla*, and *Potamethus*, Knight-Jones (1983) found a series of species which did not belong in any of them. To accommodate these species, Knight-Jones erected the new genus *Perkinsiana*.

The above diagnosis follows, for the most part, that given by Knight-Jones (1983). While *Perkinsiana* is readily distinguished from

other genera, it is not a definable group, i.e., there is no evidence to support monophyly. Essentially, species recognized in *Perkinsiana* are grouped on the basis of what they lack in comparison to other species as opposed to being defined on the basis of synapomorphy. Resolution of this problem will necessitate an in-depth comparative revision of most genera within the clade (area VII, fig. 28) defined by the occurrence of abdominal elongate, broadly hooded setae.

POTASPINA HARTMAN, 1969

TYPE SPECIES: *Potaspina pacifica* Hartman, 1969, by monotypy.

DIAGNOSIS: Medium-size sabellin species with numerous radioles; radiolar skeleton with four or more rows of cells. Palmate membrane and radiolar flanges absent. Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages present. Ventral lips and parallel lamellae present. Anterior margin of anterior peristomial ring low, of even height all around; posterior peristomial ring collar present. Inferior thoracic notosetae paleate, arranged in two or more transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior and posterior rows with elongate, broadly hooded setae in all setigers. Thoracic uncini of typical avicular form in setigers 2–4; teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. *Uncini of thoracic setigers 5–7 modified; each neuropodium with single transverse row of 3–5 thick, slightly curved, tapered spines; distal ends without dentition. Companion setae limited to setigers 2–4; distal ends as roughly symmetrical, teardrop-shaped membranes. Abdominal uncini with teeth above main fang of equal size; breast reduced to narrow swelling; long handled. Abdominal setigers numerous.*

REMARKS: *Potaspina* is characterized by the replacement of typical thoracic uncini by thick, acicular spines in posterior thoracic setigers. Concomitant with this change, I consider companion setae to have been lost in these neuropodia.

The genus was described on the basis of a single specimen. As noted by Hartman (1969), setiger 8 is incompletely formed, represented

only by notosetae on the left side. The anterior and posterior ends of the specimen do not appear to have been regenerated. Thus, the presence of neuropodial spines does not seem to be an anomaly brought on by regeneration.

The illustration of abdominal uncini provided by Hartman (1969: drawing of uncini is labeled fig. 6, but referred to as fig. 5 in the text) depicts a slightly curved, elongate handle proximal to the dentate end, without any evidence of a breast being present. Examination of the holotype reveals that the abdominal uncini closely resemble those seen, for example, in *Jasmineira*, *Fabrisabella*, and *Potamethus*; the breast is reduced to a narrow swelling and the handle below this region is sharply curved, giving uncini a Z-shaped appearance.

SABELLONGA HARTMAN, 1969

TYPE SPECIES: *Sabellonga disjuncta* Hartman, 1969, by monotypy.

DIAGNOSIS: Slender, medium-size sabellin species. Branchial crown and most associated structures unknown. Remnants of ventral lips and/or parallel lamellae present on either side of mouth, continuing posteriorly to presumed ventral sacs. Posterior peristomial ring smooth, rounded anteriorly; anterior peristomial ring not discernible. Posterior peristomial ring collar present. Inferior thoracic notosetae (setigers 2–13) paleate, arranged in two transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior and posterior rows with elongate, broadly hooded setae in all setigers. Thoracic uncini with teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends as roughly symmetrical, teardrop-shaped membranes. Abdominal uncini of typical avicular shape except in last five setigers; teeth above main fang of equal size; breast well developed, expanded; long handled. *Abdominal uncini of last five setigers replaced by large, falcate acicular spines*. Abdominal setigers numerous.

REMARKS: Hartman (1969) established *Sabellonga* (and the family Sabellongidae) on the basis of the presumed presence of spioniform palps on the "prostomium." Her evi-

dence included the presence of "palp scars." Important also was the occurrence of large, falcate notopodial spines in the last five abdominal setigers. As discussed in the cladistic results section earlier, Hartman misinterpreted the ventral lips (or perhaps ventral sacs) as palp scars.

Although *Sabellonga* is known only from one complete specimen (except for the presumed missing branchial crown) and several posterior ends, the genus appears to be well defined by the presence of falcate spines on the posterior abdomen. In addition, *Sabellonga* is unusual in that median abdominal setigers are much longer than wide, giving the animal a very slender, elongate appearance which is not characteristic of most sabellid genera. This unusual body shape was another reason for Hartman's decision to recognize the species in a separate family (K. Fauchald, personal commun.).

PSEUDOPOTAMILLA BUSH, 1905

TYPE SPECIES: *Amphitrite reniformis* Brugiere, 1789, by original designation.

DIAGNOSIS: Medium-size sabellin species with numerous radioles; outer radiolar margins appear quadrangular in shape; radiolar skeleton with four or more rows of cells. Palmate membrane and radiolar flanges absent. Unpaired, compound radiolar eyes on all radioles except dorsalmost pair and some ventralmost radioles; usually limited to proximal half of radioles. Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages present. Dorsal, marginal branchial base flanges present. Ventral lips and parallel lamellae present. Anterior margin of anterior peristomial ring low, of even height all around; posterior peristomial ring collar present. Inferior thoracic notosetae paleate, arranged in two or more transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior and posterior rows with elongate, broadly hooded setae in all setigers. Thoracic uncini with teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends as roughly symmetrical, teardrop-shaped membranes. Abdominal uncini with teeth above main fang of equal size; breast well devel-

oped, expanded; handles long. Abdominal setigers numerous.

REMARKS: *Pseudopotamilla* is most closely related to *Eudistylia* and *Schizobranchia* in that all have unpaired, compound radiolar eyes along the proximal regions of some radioles and dorsal, marginal branchial base flanges. *Pseudopotamilla* differs from *Eudistylia* and *Schizobranchia* in having what appear to be outer radiolar margins sharp-edged rather than rounded, as present in the two latter genera. The radioles of *Pseudopotamilla* are not arranged in a spiral pattern. *Eudistylia* has traditionally been distinguished by the spiral condition of the radioles, whereas *Schizobranchia* has dichotomously branched, nonspiraled radioles.

Based on the above diagnosis, *Pseudopotamilla* is not defined by any synapomorphies. As can be shown from the diagnoses for *Eudistylia* and *Schizobranchia* (given below), a revision of this sister-group complex must take into consideration the definitional problems of all three genera.

EUDISTYLIA BUSH, 1905

TYPE SPECIES: *Sabella vancouveri* Kinberg, 1867, by original designation.

DIAGNOSIS: Medium- to large-size sabellin species with numerous radioles arranged in spiral configuration; outer radiolar margins rounded; radiolar skeleton with four or more rows of cells. Radioles sometimes dichotomously branched in large individuals. Unpaired, compound radiolar eyes present on all but ventralmost radioles; limited to proximal half of radioles. Palmate membrane and radiolar flanges absent. Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages present. Ventral lips and parallel lamellae present. Dorsal, marginal branchial base flanges present. Anterior margin of anterior peristomial ring low, of even height all around; posterior peristomial ring collar present. Inferior thoracic notosetae paleate, arranged in two or more transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior and posterior rows with elongate, broadly hooded setae in all setigers. Thoracic uncini with teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends

as roughly symmetrical, teardrop-shaped membranes. Abdominal uncini with teeth above main fang of equal size; breast well developed, expanded; long handled. Abdominal setigers numerous.

REMARKS: *Eudistylia* has traditionally been distinguished from similar genera (*Pseudopotamilla* and *Schizobranchia*) by spiraling of the branchial lobes. Hartman (1938: 21) stated in her diagnosis that concerning the branchial lobes, "their ventral ends [are] free and turned inward, or spirally coiled." As in other genera in which spiraling can occur, the degree of spiraling is probably size related. This was pointed out by Perkins (1984: 295): "It is likely that some small specimens from the northeast Pacific Ocean referred to *Pseudopotamilla* are conspecific with large specimens referred to *Eudistylia*." Small specimens identified as *E. vancouveri* examined in the USNM collections do not display spiraling. If, however, spiraling is a consistent feature in sexually mature individuals, there is potential for its use as a defining quality. The problem is that the degree to which this character varies has not been taken into account in this genus.

T. H. Perkins (personal commun.) has also suggested that the nature of the branchial crown in *Eudistylia* may not be the result of spiraling, but of radiole crowding due to radioles growing over and under one another. The placement of radioles several rows deep could lead to the impression of coiling. This feature needs to be investigated further.

Bush (1905), Hartman (1938, 1942), and Banse (1979) have stated that some specimens of *Eudistylia* have radioles with single bifurcations, the condition being infrequent within and among species. While *Eudistylia* may be regarded as monophyletic on the basis of presumed spiraled branchial lobes, the presence of branching radioles creates potential problems for defining *Schizobranchia*. The presence of radioles with single bifurcations in some *Eudistylia* species approaches the condition seen in the *S. insignis*-*S. dubia* complex (see below).

SCHIZOBRANCHIA BUSH, 1905

TYPE SPECIES: *Schizobranchia insignis* Bush, 1905, by original designation.

DIAGNOSIS: Medium- to large-size sabellin

species with numerous radioles; outer radiolar margins rounded; radiolar skeleton with four or more rows of cells. Some or all radioles branched to some extent. Unpaired compound radiolar eyes present on all but ventralmost radioles; limited to proximal half of radioles. Palmate membrane and radiolar flanges absent. Dorsal lips with dorsal radiolar appendages; dorsal pinnular appendages present. Ventral lips and parallel lamellae present. Dorsal, marginal, branchial base flanges present. Anterior margin of anterior peristomial ring low, of even height all around; posterior peristomial ring collar present. Inferior thoracic notosetae paleate, arranged in two or more transverse rows. Abdominal neurosetal fascicles with two transverse rows of setae: anterior and posterior rows with elongate, broadly hooded setae in all setigers. Thoracic uncini with teeth above main fang of equal size; hood absent; breast well developed, expanded; handles of medium length. Companion setae with distal ends as roughly symmetrical, teardrop-shaped membranes. Abdominal uncini with teeth above main fang of equal size; breast well developed, expanded; long handled. Abdominal setigers numerous.

REMARKS: *Schizobranchia* has been distinguished from the closely related genera, *Pseudopotamilla* and *Eudistylia*, by the consistent occurrence of dichotomously branched radioles. As noted in the Remarks for *Eudistylia*, the status of *Schizobranchia* is questionable if considered by this single character. More well-defined relationships within the *Eudistylia-Schizobranchia* species complex may be established once the ontogenetic pattern of radiole branching has been determined in conjunction with size increase.

For example, it might be predicted that if earlier branching occurs in ontogeny, possibly coupled with large body size, there is a greater chance of compound branching taking place in a large number of radioles, as seen in *Schizobranchia insignis*. *Schizobranchia dubia* Bush has been reported to display a modification of this pattern. According to Bush (1905), *S. dubia* is smaller than *S. insignis*; the former species has both branched (only as simple bifurcations) and unbranched radioles. In her revision of the genus, Hartman (1942) maintained these two species in part on the basis of this difference in branching, and in the nature of tube formation. Berkeley and Berkeley (1950) placed the two species into synonymy, stating that degree of radiolar branching and tubes is so variable that distinctions cannot be made. They did not state to what degree branching is size related.

If extent of branching is size related, and if the onset of branching can be delayed, fewer bifurcations would be present. This might be occurring in *Eudistylia*, where only the largest individuals of some species display occasional simple branching. I am therefore suggesting that the degree of radiolar branching between species of both genera could be viewed as a transformation series, possibly caused by heterochronic events. This interpretation maintains the hypothesis of homology of branching in these sister taxa. If radiole branching can be explained in such a manner, the validity of *Pseudopotamilla*, *Eudistylia*, and *Schizobranchia* as separate genera is open to question. Such an analysis should be made at the specific level, including all species from the three genera.

KEY TO GENERA OF THE REVISED SABELLIDAE INCLUDED IN THE PRESENT STUDY

- 1a. Thoracic uncini absent *Caobangia*

b. Thoracic uncini present 2

2a. Breast of thoracic uncini narrow, poorly developed, giving uncini an acicular appearance 3

b. Breast of thoracic uncini well developed, giving uncini a Z-shaped, or avicular appearance 16

3a. Abdominal uncini rasp-shaped plates, with
- an elongate manubrium below dentate region 4

b. Abdominal uncini rasp-shaped plates, or with series of teeth above a main fang, but without a manubrium 9

4a. Ventral filamentous appendages present . 5

b. Ventral filamentous appendages absent ...

..... *Fabricia*

- 5a. Ventral filamentous appendages vascularized 6
- b. Ventral filamentous appendages nonvascularized *Fabriciella*
- 6a. Ventral filamentous appendages unbranched 7
- b. Ventral filamentous appendages branched *Augeneriella*
- 7a. Dorsal lips present; teeth above main fang of thoracic uncini of equal size 8
- b. Dorsal lips absent; teeth above main fang of thoracic uncini unequal in size . Genus B
- 8a. Body surface, especially radioles and pygidium, with minute, emergent spicules; anterior peristomial ring modified ventrally as a thick, rounded lobe; three pairs of pinnulate radioles Genus A
- b. Body surface without spicules; anterior peristomial ring modified as a thin collarlike membrane; two pairs of pinnulate radioles *Manayunkia*
- 9a. Abdominal uncini as rasp-shaped plates only 10
- b. Abdominal uncini at least in part not rasp-shaped, with a distinct main fang surmounted by broad series of smaller teeth 11
- 10a. Posterior peristomial ring collar present; anterior peristomial ring with a narrow, triangular, ventral lobe *Oriopsis*
- b. Posterior peristomial ring collar absent; anterior peristomial ring with a wide, blunt, ventral lobe *Desdemona*
- 11a. Abdominal uncini form short, discrete tori 12
- b. Abdominal uncini form nearly complete cinctures around the body ... *Myxicola*
- 12a. Abdominal uncini with a distinct handle proximal to the breast 15
- b. Abdominal uncini without a distinct handle 13
- 13a. Thoracic neuropodial companion setae present *Panousea*
- b. Thoracic neuropodial companion setae absent 14
- 14a. Last several abdominal setigers modified as a ventral anal depression *Euchone*
- b. Last several abdominal setigers resemble more anterior setigers *Chone*
- 15a. Palmate membrane present; dorsal radiolar appendages and bayonet setae absent ... *Fabrisabella*
- b. Palmate membrane absent; dorsal radiolar appendages and bayonet setae present ... *Jasmineira*
- 16a. Handle of thoracic uncini very long *Potamethus*
- b. Handle of thoracic uncini of medium to short length, or absent 17
- 17a. Abdominal neuropodial tori as erect, conical lobes 18
- b. Abdominal neuropodial tori as low, transverse ridges 22
- 18a. Companion setae present 19
- b. Companion setae absent 20
- 19a. Radiolar eyes absent; abdominal neurosetae arranged in a tight spiral pattern *Sabella*
- b. Radiolar compound eyes present; abdominal neurosetae arranged in an incomplete spiral, or C-shaped pattern *Bispira*
- 20a. Outer margins of radioles with stylodes ... 21
- b. Outer margins of radioles without stylodes *Sabellastarte*
- 21a. Stylodes poorly developed, only as low, rounded elevations; radiolar eyes absent *Pseudobranchiomma*
- b. Stylodes well developed; paired, radiolar compound eyes present ... *Branchiomma*
- 22a. Abdominal neurosetae include paleate setae 23
- b. Abdominal neurosetae do not include paleate seta 25
- 23a. Posterior peristomial ring with large, erect, dorsal and ventral flanges ... *Anamobaea*
- b. Posterior peristomial ring without such appendages; accessory lamellae may be present 24
- 24a. Setae of setiger 1 arranged in an elongate fascicle *Notaulax*
- b. Setae of setiger 1 arranged in a bundle similar to other superior thoracic notosetae *Hypsicomus*
- 25a. Inferior thoracic notosetae composed of broadly hooded setae 26
- b. Inferior thoracic notosetae composed of paleate setae only 27
- 26a. At least some radioles with compound eyes located on inner margins, near the distal end *Megalomma*
- b. No radiolar compound eyes present *Demonax*
- 27a. With unpaired radiolar compound eyes present on outer margins; limited to proximal region of most radioles 28
- b. Without compound radiolar eyes 30
- 28a. Radioles, at least of large specimens, appear spiraled; very numerous (>20 pairs); sometimes dichotomously branched *Eudistylia*
- b. Radioles not spiraled; less than 20 pairs ... 29
- 29a. Radioles with numerous dichotomous branches *Schizobranchia*
- b. Radioles not branched ... *Pseudopotamilla*
- 30a. Radioles united by a palmate membrane ... *Potamilla*

- b. Radioles free to their bases 31
- 31a. Thoracic neurosetae replaced by thick spines
on last few setigers *Potaspina*
- b. All thoracic neurosetae are uncini of similar
shape 32
- 32a. Last 5 abdominal setigers with uncini re-
placed by large, thick, falcate spines
..... *Sabellonga*
- b. All abdominal uncini of similar shape . 33
- 33a. Posterior peristomial ring collar present ..
..... 34
- b. Posterior peristomial ring collar absent ...
..... *Amphiglena*
- 34a. Thoracic and abdominal uncini without
handles *Laonome*
- b. Thoracic and abdominal uncini with han-
dles *Perkinsiana*

ASPECTS OF CHARACTER STATE TRANSFORMATION SERIES IN THE SABELLIDAE

Whereas systematic statements have been made for various polychaete groups, specific statements about character state transformation series have usually not been given explicitly. The adaptationist scenarios which usually follow from the use of more traditional taxonomic methods do not lead to a rigorous examination of transformation series. In general, implicit or explicit transformation series have been provided only in instances where a worker has felt that a character, or suite of characters, would further a particular intuitive view of relationship. Circularity easily enters into such an exercise in that preconceived transformation series are established to justify specific patterns of relationship. The result has been a tendency to concentrate only on phylogenetic pattern, with little or no regard for the transformation series which could substantiate such patterns.

Cladograms serve the dual classificatory function of summarizing patterns of both taxon and character state distributions. In systematics, cladograms also provide hypotheses of phylogenetic relationship based on character state transformations. While phylogenetic patterns are certainly of interest, critical testing of such hypotheses will not only come about by the introduction of new characters, but also by evaluation and reappraisal of transformation series. As working hypotheses, transformation series provide the basis for more thorough examinations of characters as well as insights into research on intrinsic (phylogenetic) or developmental constraints, ontogenetic changes, and general mechanisms necessary for the coordination of character state distributions associated with body form or body regionation.

Like a number of polychaete families, the Sabellidae display distinct body regionation in the form of a thorax and abdomen. Transition between these areas in the Sabellariidae, Sabellidae s.l., and Serpulidae s.l. is indicated by setal inversion, and also in the latter two families (although very modified in *Caobangia*) by a shift in the fecal groove from a midventral position in the abdomen to middorsal in the thorax. Sabellids consistently display a thorax and abdomen, but with the number of setigers in each area sometimes being variable between genera (e.g., Knight-Jones, 1981). Most workers have noted distinct concordance between these regions and setal forms.

For instance, the old concept of the Fabriciinae (sensu Johansson, 1927 or Rioja, 1923) was based in part on the different shapes of thoracic and abdominal uncini. Such observations might suggest that general regions of thorax and abdomen may in some way influence lower-level conditions, e.g., similar setal forms, resulting in the appearance of an organism with numerous yet distinctive sets of thoracic and abdominal segments. Based on the present transformation series, the inferred levels of influence on setal type over the length of the body appear to be quite variable. It appears that control of setal form distribution can be regulated within or between regions and is to some extent independent even between notopodia and neuropodia of the same segment. The point to be made here is that developmental constraints are probably operating at a series of hierarchical-morphological levels in setal formation and not simply at the level of the chaetoblast or support cell. The hypotheses of transformation series presented above and

discussed below could provide the framework for investigations into mechanisms limiting patterns of setal formation.

The following discussion will concentrate on aspects of setal transformation series, comprising characters 28–39 and 41–43. Within inferior thoracic notosetal fascicles and abdominal neurosetal fascicles, the anterior and posterior setal groups are here examined as single groups comprising covarying units. Characters constituting thoracic and abdominal uncini are discussed in the context of uncini being entire entities, but with areas which covary independently. Character state changes are the same as those given on the cladograms (figs. 28–30, see also Appendix II).

INFERIOR THORACIC NOTOSETAL FASCICLES (CHARACTERS 28–31)

The different inferior notosetal characters include observations on anterior and posterior setal groups as well as any setal changes in the thorax (see Appendix II) of both anterior and posterior groups. Figure 32 summarizes the covarying character state changes of both groups. Inferior thoracic notosetae differ markedly from similarly hooded abdominal neurosetae in that the degree of within-thorax setal variation is comparatively slight. Only in Genus A and the *Fabriciola*–Genus B–*Fabricia*–*Augeneriella* clade (area I) are there any setal changes occurring between thoracic setigers.

The plesiomorphic condition within the Sabellidae appears to be fascicles consisting of only an anterior setal group composed of elongate, narrowly hooded setae. The transition of this state to broadly hooded or pseudospatulate in some median setigers is seen in some of the fabriciina genera, listed above, in area I.

Within the area II–VII clade, the most plesiomorphic condition appears to be modification of the elongate, narrowly hooded state to the bayonet form, as seen in *Desdemona* and *Oriopsis*. A transitional stage follows in which a posterior setal group has been added in the series. Setae in this posterior group are paleate, with this arrangement found in *Chone*, *Panousea*, and *Jasmineira*. In *Euchone*, the paleate state has been slightly

modified to a broadly hooded form, which appears similar to that seen in *Megalomma* and *Demonax*. The anterior bayonet setal group has been lost in remaining sabellina genera, with paleate setae representing the most common state for the posterior group. From the paleate form can be derived two different states: spinelike, in such genera as *Sabella*, *Bispira*, and *Branchiomma*; and broadly hooded, in *Demonax* and *Megalomma*.

Hypotheses of inferior thoracic notosetal evolution have usually not been made explicitly, probably because most authors did not distinguish between superior and inferior groups. Rioja (1929, 1931), however, suggested that the elongate, narrowly hooded state (his “limbate capillaries”) is primitive. I suspect that Rioja’s view stems from the idea that a narrowly hooded condition is in some way less complex, or less “specialized,” than other states. Similar views have been expressed by Streltsov (1973) for the Paraonidae, Holthe (1986) for the Terebellomorpha (= Terebellida), and Rosenfeldt (1982) and ten Hove (1984) for serpulids. Gee (1964) and Pillai (1970) used the criterion that “common equals primitive” in establishing transformation series for certain serpulid setal forms. In the present study, designation of the elongate narrowly hooded state as plesiomorphic was not made on the basis of equating “simplicity” with primitiveness, but as a result of outgroup comparison.

Structurally, emergent parts of sabellid hooded setae appear to have a very consistent form, being composed of (1) a dense shaft which is distally variably surrounded by (2) a thin, hoodlike structure formed of microtubules, and (3) with lacunar spaces between the hood and shaft. Transformation from one state to another appears to be accomplished simply by changing relative shapes of the shaft and hood. As a result, it would be difficult to justify considering one state as “simple” as opposed to “complex” on the basis of shape alone. The relationship of shaft, hood, and lacunae were cursorily examined by Perkins (1984).

The present study hypothesizes that broadly hooded setae of *Demonax* and *Megalomma*, and spinelike setae are derived from the paleate state (fig. 32). Based on the micrographs of setal cross sections given by Perkins

Characters 32–35 comprise such features as the presence or absence of anterior and

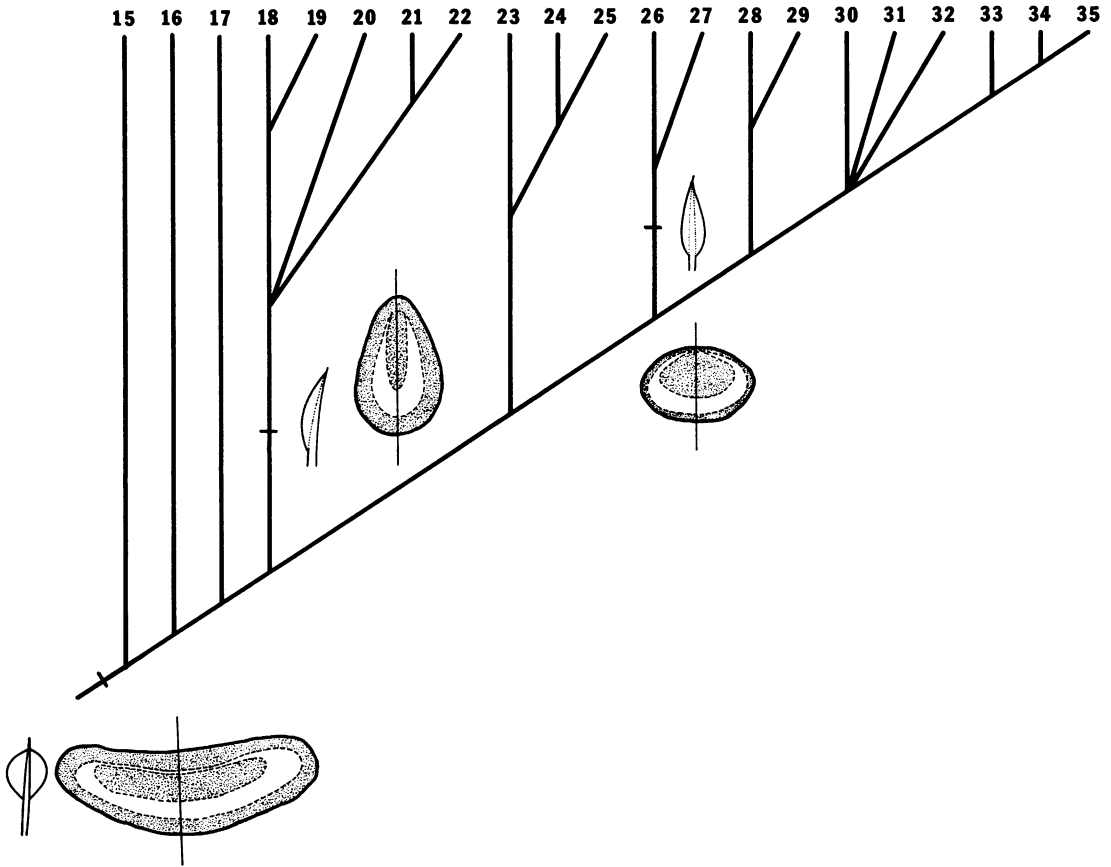


Fig. 33. Section of cladogram 1 (see figs. 28 and 32) with transformation series for paleate, spinelike, and broadly hooded setae, with schematic representations of cross sections through the midsection of each. Cross sections are oriented in the same direction (modified from Perkins, 1984: fig. 1). Genera are numbered as in figure 28.

posterior setal rows in a fascicle, and distinctions between far anterior and posterior fascicles. As is the case with thoracic noto-setae, all sabellid abdominal neurosetae are hooded. Hypotheses of transformation have apparently not been presented, probably owing to incomplete characterizations of possible setal types.

Figure 34 presents a summary of transformations for anterior and posterior setal rows in anterior and posterior regions. In general, the most striking difference between thoracic and abdominal hooded setae is the greater tendency for regional setal variation in the abdomen. The plesiomorphic condition in both thorax and abdomen appears to be the presence of a single transverse row of hooded setae. In the apomorphic condition, however,

with the addition of another row, the original (plesiomorphic) rows are situated anteriorly in the thorax and posteriorly in the abdomen.

In the most plesiomorphic condition, the single (posterior) abdominal row is composed of modified, elongate, narrowly hooded setae. This is seen in all fabriciins (except *Caobangia*) and the sabellins, *Desdemona* and *Oriopsis*. From this plesiomorphic condition are derived two rows per fascicle in all abdominal setigers, which is common to most remaining sabellin genera. The initial transformation from single to double rows is accomplished by the addition of an anterior row of elongate, narrowly hooded setae in anterior setigers, while modified, elongate, narrowly hooded setae comprise both rows in posterior setigers.

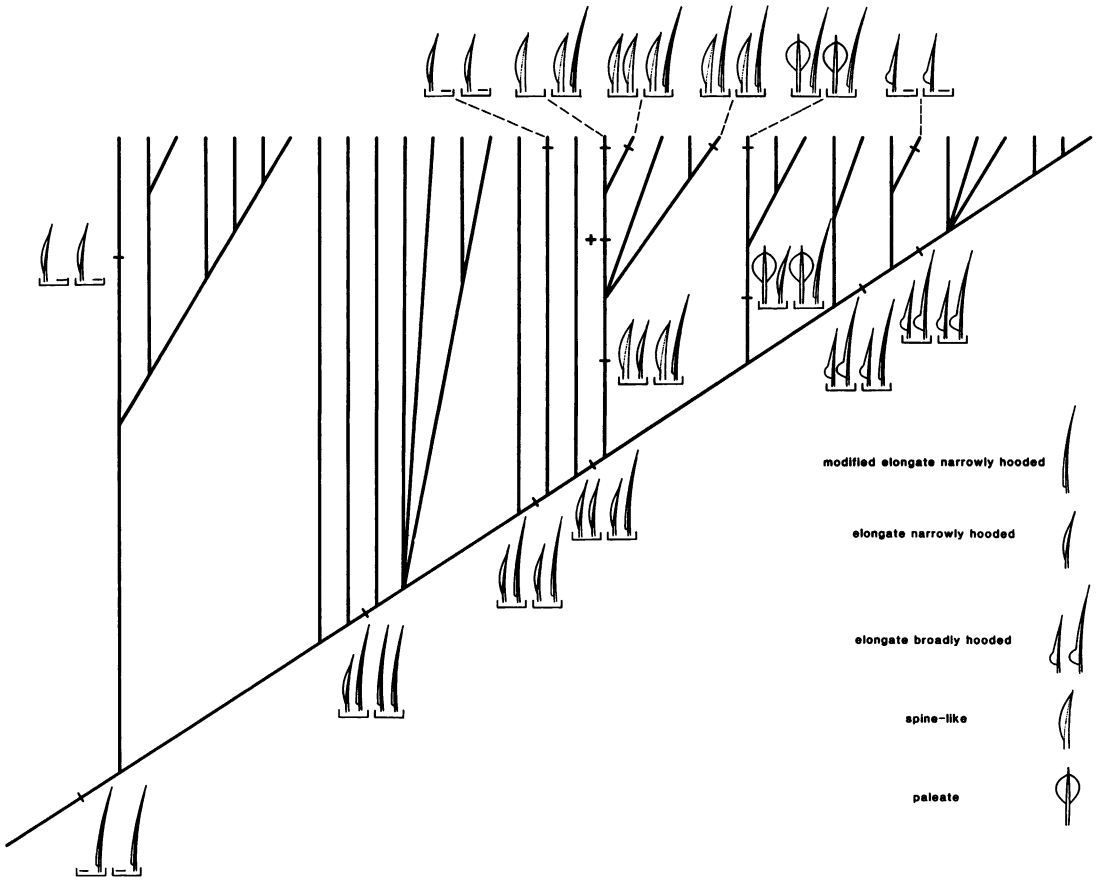


Fig. 34. Schematic representation of transformation series for abdominal neurosetal fascicles in cladogram 1 (fig. 28). Both setal rows within anterior (left) and posterior (right) fascicles are bracketed, respectively. Transformation series are the same in all cladograms. The “+” on the stem leading to *Sabella* and *Bispira* refers to the possibility of three equally parsimonious conditions on that stem, i.e., either one of the arrangements seen in *Sabella* or *Bispira*, or on the next most plesiomorphic stem (see also fig. 28).

The distribution pattern in posterior abdominal setigers is then altered such that the anterior row of modified, elongate, narrowly hooded setae are transformed to elongate, narrowly hooded setae (e.g., *Potamethus*). Next is the derivation of elongate, narrowly hooded setae in the posterior row of anterior fascicles from modified, elongate, narrowly hooded. Thus, there is a trend toward transformation in an anterior-posterior direction, both with respect to setigers and fascicles.

From the apomorphic condition of anterior fascicles with two rows of elongate, narrowly hooded setae and posterior fascicles with elongate, narrowly hooded and modified, elongate, narrowly hooded, are derived

three major distribution patterns. These changes are primarily transformation of anterior setal rows throughout the abdomen in three monophyletic clades; the elongate, narrowly hooded state is transformed to either spinelike, paleate, or elongate broadly hooded. Within some of these clades, there is also a tendency toward transformation of the posterior setal row in anterior and posterior setigers to the setal form seen in the adjacent anterior row. The main exception to this tendency is in *Anamobaea*, *Hypsicomus*, and *Notaulax*, where paleate setae are only found in anterior setal rows of each fascicle.

In comparing transformation series of inferior thoracic notosetae with abdominal

neurosetae, there are a number of instances of convergence. For example, thoracic spine-like setae are hypothesized to have been uniquely derived from paleate setae (e.g., *Sabella*, *Bispira*, *Branchiomma*). Within the same monophyletic group, abdominal spine-like setae are always present, at least in anterior setal rows of all setigers, but are derived from elongate, narrowly hooded setae. Similarly, results indicate that thoracic paleate setae were already present in the ancestor which gave rise to *Anamobaea*, *Hypsicomus*, and *Notaulax*; the abdominal paleate setae of these genera are hypothesized to have been derived from elongate, narrowly hooded setae.

Convergence of forms between abdominal setal rows is also suggested. For example, a number of genera (e.g., *Potamilla*, *Pseudopotamilla*, *Eudistylia*) possess only elongate, broadly hooded setae in both setal rows throughout the abdomen. The present transformation series, however, indicate that setae of all anterior setal rows are derived from the elongate, narrowly hooded state while posterior rows in posterior setigers are derived from modified, elongate, narrowly hooded setae.

The apparent transformation series for thoracic and abdominal hooded setae indicate that there is a great deal of structural lability in the formation of both shaft and hood. Comparatively, the degree of change seen in the abdomen overall is far greater than that seen in the thorax, suggesting that there are segregated mechanisms regulating hooded setal formation in thoracic and abdominal areas. This generalization does not, however, appear valid for genera with spine-like or paleate setae in both the thorax and abdomen. Instead, there appears to be some degree of uniform regulation of setal form throughout the body, allowing for similar states to be derived from different plesiomorphic conditions.

Research pertaining to the phenomenon of sabellid body regionation, or axial polarity, has been concentrated on regeneration phenomena (e.g., Fitzharris, 1973, 1976). These studies demonstrate that the ventral nerve cord produces neurosecretory granules which dictate differentiation of thorax and abdomen. An axial concentration gradient exists

in which high concentrations of neurohormone elicit formation of thoracic segments and lower concentrations, below a particular threshold level, induce formation of abdominal segments. In this regard, it would appear that setal formation might be under regional control. Unfortunately, the possibility of interaction of chaetoblast and supporting cells with neurohormones has not yet been investigated. Such research would need to take into consideration that abdominal setal form may be uniform throughout or display regional variation in an anterior-posterior direction.

In his observations of growth in several sabellid species, Berrill (1977a, 1977b) suggested that regulation of thoracic and abdominal setiger formation is under two distinct controls. Berrill (1977b) noted, however, in some species [i.e., *Branchiomma nigromaculata* (Baird), *Potamethus elongatus* (Treadwell), and an unidentified "dwarf" species] that the later addition of posterior thoracic setigers is accomplished by the transformation of anterior abdominal setigers. During transformation, abdominal notosetae and neurosetae are lost, with subsequent emergence of thoracic setae in the typical inverse position. At this time it is not known how such transformation is induced. Three questions must be considered with regard to these setal changes: (1) during transformation, do the original setal tissues degenerate, with new thoracic setal tissues forming, (2) do the original abdominal setal tissues migrate to inverse positions and continue producing their respective setal forms, or (3) do setal tissues remain in place during transformation and only begin producing thoracic-type setal forms? While the mechanism(s) which initiates these transformations is still not known, such changes could conceivably be explained by the model developed by Fitzharris (1973, 1976), discussed above. Answers to the questions listed above might explain some of the setal distribution patterns seen in the present study.

Present results do agree in a restricted sense with the more general views of workers such as Fitzharris (1973, 1976) and Berrill (1977b), i.e., that morphogenetic properties operate separately, one at the level of the thorax and another for the abdomen, inducing formation of similar segments, setae, etc., in a particular

region. In this sense, hooded setal structure and setal distributions are determined throughout the thorax or abdomen by the same morphogenetic mechanisms which induce the overall formation of thorax and abdomen. Present results also suggest that controlling factors at the level of the entire thorax/abdomen can also determine setal formation, resulting in the same setal form occurring in both regions, but derived from completely different plesiomorphic states.

A third pattern of variability may also be recognized, in which there are clear differences between anterior and posterior abdominal fascicles. This is seen, for example, in *Euchone*, *Chone*, *Panousea*, and *Jasmineira*, where in anterior setigers the anterior setal row is composed of elongate, narrowly hooded setae, but in far posterior setigers this form is replaced by modified, elongate, narrowly hooded setae. As a consequence of this phenomenon, in more apomorphic genera the plesiomorphic state of modified, elongate, narrowly hooded setae is limited to the posterior setal row of only far posterior setigers.

While a proximate causal explanation cannot be given at this time, the trend may be, in part, a growth phenomenon. Since the addition of segments always occurs from a growth zone just in front of the pygidium, the anteriormost abdominal setigers are oldest, becoming younger in a posterior direction. As segments age, setae may be shed, with chaetoblasts producing new forms. For example, Fredette (1982) and George (1984) observed that as capitellid polychaetes added setigers during juvenile growth, hooded hooks are shed in some anterior setigers and replaced with "limbate capillary" setae. A somewhat similar phenomenon has been noted for changes in abdominal uncini by Banse (1970, 1972) in *Chone* and *Euchone* (see next section).

Thus, the type of abdominal setal variation displayed may in part be a function of segment age. This might explain the fact that the transition from, say, elongate narrowly hooded to modified, elongate, narrowly hooded in an anterior-posterior setiger direction appears to be relatively gradual. If there is a gradient effect operating in some sort of setal regulatory control(s), then segment age or consequent location along the body may be

the determinants of what setal types are capable of being retained. Varying the extent of such age-dependent and location-dependent control(s) takes into account the fact that large-bodied species of *Euchone*, *Chone*, and *Jasmineira* still possess modified, elongate, narrowly hooded setae in anterior setigers, whereas similarly sized species of *Demonax* and *Megalomma* have replaced this state with elongate, narrowly hooded setae.

THORACIC AND ABDOMINAL UNCINI (CHARACTERS 36–39 AND 41–43)

By nature of their general shape and distinctive dentition, uncini have sometimes been regarded as important features for inferring relationships at various levels. Apparently the degree to which transformation series and polarity could be established was viewed as being more straightforward with this setal form than with hooded setae. In the present study, characters 36–39 comprise thoracic uncinal features, while characters 41–43 describe states for abdominal uncini.

As noted earlier, the traditional designations of "acicular" or "avicular" were not applied in the cladistic analysis since these terms are vague descriptions which hinder rather than help provide accurate descriptions of these structures or their transformation series. Application of these terms in the present discussion (and diagnoses above) is meant as a shorthand way of referring to general features of breast and handle development in light of the descriptions provided above of each character state. A more specific terminology for categorizing uncinal types has been suggested by Holthe (1986), who also recognized the need for establishing transformation series for various uncinal regions (see also Rosenfeldt, 1982).

If an uncinus is regarded as an entity composed of a group of covarying regions (= states), it is then possible to view general shape changes of entire thoracic or abdominal uncini as a function of these sets of transformation series. Figure 35 is a schematic illustration of thoracic and abdominal uncinal forms based on the transformation series for most uncinal characters.

The Sabellidae s.l. differ from the Serpulidae s.l. in that thoracic uncini of the former

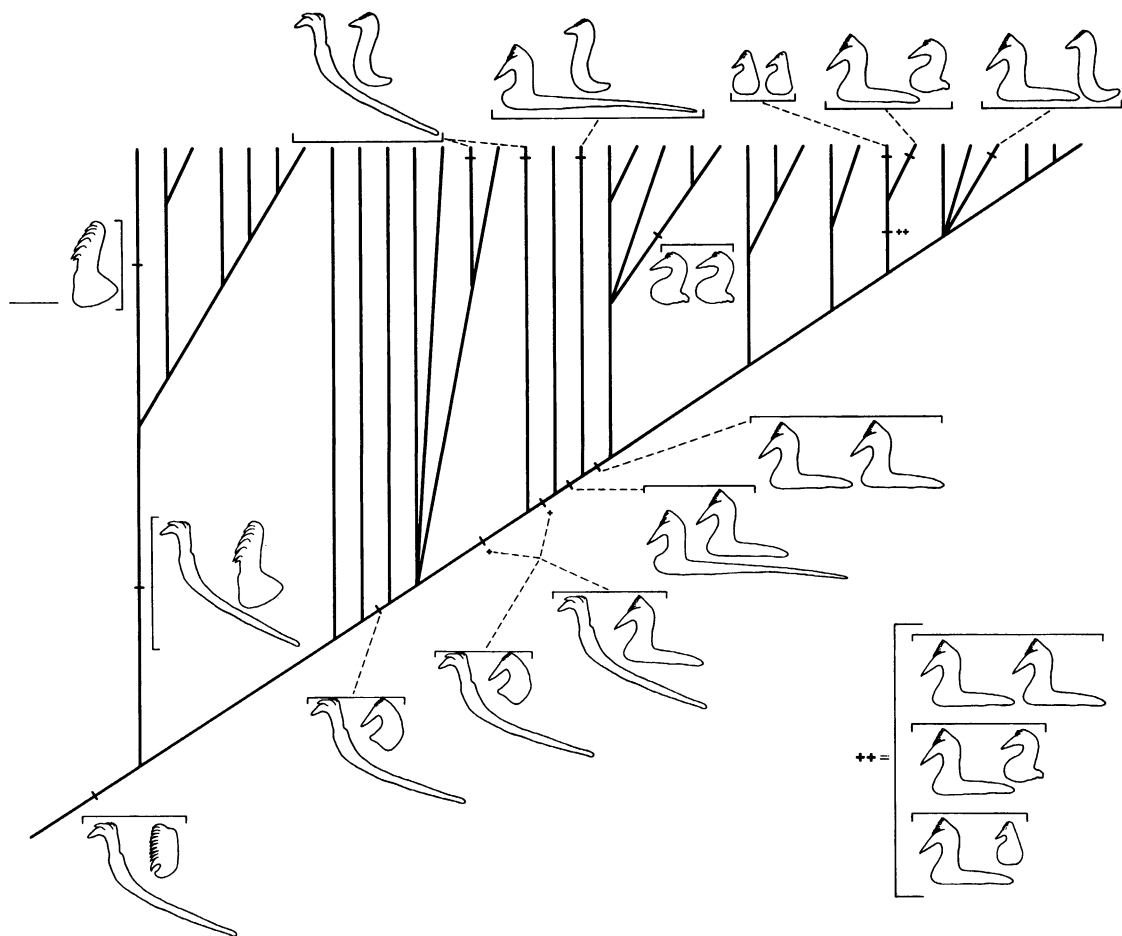


Fig. 35. Schematic representation of transformation series for thoracic and abdominal uncini. Thoracic uncini are to the left, abdominal uncini to the right, within a given bracket. Cladogram 1 is shown; transformation series are the same in all cladograms except in the case of area IIb (see text for explanation). The two instances in which there is ambiguity as to possible nodal conditions are indicated by a "+" and "++", respectively.

(absent in *Caobangia*) always have a main fang surmounted by a broad series of smaller teeth as well as a proximal handle (which is lost in *Laonome*). While serpulids characteristically have similar thoracic and abdominal uncini in the form of rasp-shaped and/or saw-shaped plates, sabellids display a much greater variety of uncinal shapes. Probably the most striking aspect of these transformation series is the fact that, as in the case of hooded setae, sabellid thoracic and abdominal uncini display some degree of independence with regard to transformational tendencies and degree of structural lability. Likewise, present

hypotheses also suggest convergence of uncinal form between the two regions.

Based on figure 35, the most plesiomorphic condition is that in which genera display acicular thoracic uncini, i.e., a long handle and poorly developed breast, and abdominal rasp-shaped plates, also with a poorly developed breast. The thoracic acicular condition is present in the fabriciina genera (area I; lost in *Caobangia*) and the more plesiomorphic genera of the revised Sabellinae (areas II–VII). In the same groups, modification of abdominal uncini has occurred in two major directions. In the fabriciina genera, the abdominal

uncinal breast has expanded into a distinct manubrium, while in all Sabellinae genera apomorphic to *Desdemonia* and *Oriopsis*, the rasp-shaped condition has been modified such that there is now a broad series of small teeth above a main fang and the breast has become enlarged. In this latter group, thoracic and abdominal uncini resemble one another at least with regard to dentition.

The next step in the transformation of abdominal uncini has occurred several times, as seen in the Sabellinae genera, *Jasmineira* and *Fabrisabella*. Both genera have typical thoracic acicular uncini, but the abdominal uncial breast has elongated and narrowed, and a handle has developed. Similar abdominal uncini are found in *Potamethus* and *Potaspina*. The plesiomorphic condition from which these forms are derived is ambiguous to some extent [indicated by the plus (+) in fig. 35; see also area IIb, fig. 29A]. While the handles of abdominal uncini may be derived several times, it is hypothesized that development of the handle on uncini with a well-developed breast is the plesiomorphic condition for the remaining Sabellinae genera.

Development of a form transitional between the typical thoracic acicular and avicular form is represented in *Potamethus*. This condition could have been derived from expansion of the breast in acicular uncini, which closely resemble the avicular form except for the very long handle. This part of the transformation series may, however, be inaccurate since there are some species of *Potamethus* which have a more typical acicular form (cf. Knight-Jones, 1983).

One of the features uniting genera within the old concept of Sabellinae has been the fact that thoracic and abdominal uncini display similar avicular forms, i.e., an expanded breast and medium-length (or shorter) handle. Based on the present transformation series, the typical avicular shape has been derived from different forms in the thorax and abdomen, respectively. Thoracic avicular uncini can be arrived at via shortening of the handle of *Potamethus*-type uncini. A similar abdominal form is derived from the plesiomorphic state by development of a handle (e.g., in *Jasmineira*, *Fabrisabella*, and *Potamethus*). In this respect, thoracic and abdominal uncini display a general transformational

pattern similar to hooded setae in that convergence to the same form from different combinations of plesiomorphic states in different body regions has occurred. These changes in uncial shape do not, however, parallel changes in hooded setae.

From the condition of similar thoracic and abdominal avicular uncini (with a medium-length handle) can be derived four separate trends in several taxonomic groups. In one or two of these groups there are concurrent and similar uncial changes in both body regions and two groups with only abdominal uncial changes. In the *Branchiomma*-*Pseudobranchiomma* clade, the handle of both thoracic and abdominal uncini has become shortened. A similar phenomenon has occurred in *Amphiglena*, but only with respect to abdominal uncini. Thoracic and abdominal uncini of *Laonome* resemble one another in having lost the handle. Several transformation series are possible, however, in deriving the conditions in *Laonome* and *Amphiglena* (indicated by ++ in fig. 35), such that concurrent thoracic and abdominal uncial handle loss in *Laonome* is not the only possibility. Abdominal uncini of *Potaspina* have been modified such that they resemble those of *Jasmineira*, *Fabrisabella*, and *Potamethus*.

The general trends hypothesized above for sabellid uncini are very similar to those discussed for hooded setal forms. These include (1) derivation of similar types of avicular uncini in both body regions from completely different combinations of plesiomorphic states, i.e., a thoracic acicular form and abdominal rasp-shaped plates; (2) subsequent uncial variation occurring only in the abdomen (e.g., *Potaspina* and possibly *Amphiglena*); or (3) instances of concurrent uncial variation occurring in both thorax and abdomen (e.g., *Pseudobranchiomma*, *Branchiomma*, and possibly *Laonome*). As with hooded setae, structural lability in uncial construction may be restricted to a given body region, display uniform changes throughout both regions, or show independent changes ultimately leading to similar forms.

The transformation series for uncial states that provide the patterns of change seen in figure 35 support, to some degree, past statements concerning this aspect of setal evolu-

tion. Based on his subfamily revision (Rioja, 1923), Rioja (1929, 1931) stated explicitly that the transformation of sabellid thoracic uncini occurred in a manner such that acicular uncini are plesiomorphic and from which can be derived avicular uncini. Rioja's transformation series was apparently based on the idea that the Sabellidae (and Serpulidae?) share a unique origin in common with at least some of the terebellomorphs, i.e., the Terebellidae and Trichobranchidae. Hence, the similarities in thoracic acicular uncini and some abdominal uncinal forms (see below). As noted earlier, there is at this time no firm evidence to support the view of an exclusive monophyletic relationship between the terebellomorphs and the Sabellidae-Serpulidae clade outside of the fact that both groups have uncini. Considering the fact that setal form is apparently very labile, it would seem unwise to hypothesize sister-group relationships on this suite of characters alone.

Like Rioja, Johansson (1927) hypothesized that the thoracic acicular form is a primitive one from which could be derived avicular uncini. Johansson also suggested an overall transformation series for thoracic uncini, but in which the most primitive state would have been some form of capillary setae ("Haarborsten") from which is derived companion setae. Acicular setae could then be derived from companion setae. In the context of the present study, this view presents logical problems for Johansson's ideas on the relationship of his Fabriciinae to the Sabellinae.

Based on Johansson's expressed transformation series and his statement that the Fabriciinae is more primitive than the Sabellinae, one would have to hypothesize that the sabellid ancestor at one time had two rows of companion setae. Within this ancestral form, the posterior row was then modified into acicular uncini. The ancestor giving rise to the fabriciins would then have to lose the anterior row of companion setae while the Sabellinae ancestor maintained both rows, but with the posterior row of acicular uncini transforming to avicular forms.

I have presented this scenario with the assumption that Johansson may have viewed the two subfamilies as monophyletic. Since, however, he also claimed that the Fabriciinae are more primitive than the Sabellinae, Jo-

hansson was probably thinking more in terms of the subfamilies representing grades as opposed to clades. This being the case, one would have to hypothesize that ancestral companion setae were lost in the fabriciins, then reappeared in the sabellins. Results of the present study do not support either of these views.

Knight-Jones (1981) came to a conclusion similar to that given by Rioja (1929, 1931), Johansson (1927), and the present study with regard to the general transformation from acicular to avicular thoracic uncini, citing a homologous relationship between the breast of the two forms. Knight-Jones (1981: 190) also suggested that the thoracic uncini of *Potamethus* are "intermediate between the short-shafted thoracic uncini found in most Sabellinae and those of the other subfamilies." While this is supported by the present study, Knight-Jones did not explain the basis for her statement.

The plesiomorphic condition for abdominal uncini was considered by Rioja to be that of a main fang and expanded breast, but with no handle present (e.g., *Euchone*, *Chone*, *Myxicola*). In fact, the similarity of thoracic and abdominal uncini in *Myxicola* to those of some trichobranchids and terebellids was what led Rioja to the conclusion that the Myxicolinae is the most primitive subfamily. Rioja also viewed the abdominal uncini of *Jasmineira*, considered avicular by most workers, to be an intermediate form between the abovementioned plesiomorphic form and the typical avicular uncini seen in traditional Sabellinae genera. Present results consider the form seen in *Jasmineira* to have been derived several times, and not as an intermediate form leading to avicular uncini. Rioja made no statement, however, as to where rasp-shaped uncinal forms, as seen in *Fabricia* or *Oriopsis*, would be placed in his scheme. The primary difference between the hypotheses presented here and those of Rioja lie in the nature of establishing character state polarities.

In his work on *Euchone* and *Chone*, Banse (1970, 1972) hypothesized that these two genera were in some respects transitional forms, being derived from an hypothetical ancestor with rasp-shaped abdominal uncini similar to those seen in *Oriopsis*, yet plesiomorphic to genera which were usually considered in the Sabellinae (fig. 9). Banse based

his view on the fact that in many species of *Euchone* and *Chone* at least some uncini in posterior setigers are in the form of rasp-shaped plates, whereas anterior setigers have more typical uncini with a main fang and expanded breast. Banse noted that rasp-shaped forms were situated dorsalmost in a torus, thus being formed first ontogenetically. Such ontogenetic precedence, and the fact that rasp-shaped uncini also occur in other sabellid genera and other families, led Banse to conclude that this uncinal form is more primitive than other abdominal forms.

In the present study, the kinds of variable conditions seen by Banse were not included for several reasons: (1) an attempt was made to limit taxonomic considerations as much as possible to only type species; (2) the phenomenon described by Banse (1970, 1972) is not found in all species of either *Chone* or *Euchone* (including the type species); and (3) there is some doubt as to the monophyly of *Chone*.

Although the ontogenetic sequence of abdominal setal change noted by Banse was not taken into consideration here, the transformation from a rasp-shaped uncinal form to the more typical *Chone* or *Euchone* form is substantiated by other character-state transformation series. In addition, the relationship of these two genera to other sabellids is very similar to the view expressed by Banse (1970; see fig. 9).

In the previous section, discussing abdominal hooded neurosetae, I suggested that the presence of some setal forms in far posterior abdominal setigers may be due to the relative age and location of those segments, with young setigers producing one setal form which may be later replaced by another form. For example, I suggested that this might provide a partial explanation for the pattern of loss of modified, elongate, narrowly hooded setae in anterior setigers in the larger-bodied, more apomorphic genera. This same situation appears to present itself with the abdominal uncini of some *Euchone* and *Chone* (e.g., Banse, 1970, 1972).

The presence of rasp-shaped uncini in far posterior setigers is explicable as being an ontogenetic phenomenon. If the first uncini produced are rasp-shaped (e.g., Okuda, 1946), and then they are gradually replaced by un-

cini with a main fang surmounted by a broad series of smaller teeth and with an expanded breast, it might be expected that some of the far posterior, thus youngest, setigers would still possess rasp-shaped uncini. The older the setigers, the greater the tendency for loss of the earliest formed uncini. The degree to which such uncini might be maintained in more anterior setigers, such as in *Euchone hancocki* Banse, is probably related to some form of epigenetic regulation of setal formation, as discussed above.

One of the problems in dealing with metameric forms is the fact that different body regions may not display uniform distributions of a given state owing to segmental age or location differences, and the degree to which regulatory mechanisms may impinge on the expression of such states. These considerations need to be explored further in order to interpret present results more fully.

The general patterns of transformation series presented above do not agree with the results presented by Rosenfeldt (1982). In this latter study, uncini from the following families were examined: Maldanidae, Pectinariidae, Ampharetidae, Terebellidae, Sabellariidae, Sabellidae, and Serpulidae. Rosenfeldt (1982: 268) stated that these families are of a "monophyletic origin" since they all have similar uncinal forms. Transformation series for uncini were suggested for each family, established on the basis that the ancestral uncinal form displayed a main fang surmounted by a single arc of very small teeth. From this plesiomorphic state is derived what Rosenfeldt interpreted to be four different states, which displayed variations in dentition from the original ancestral form.

Because of the small number of states distributed among a large number of genera, there are a number of instances of inferred convergence. This led Rosenfeldt (1982: 268) to conclude that "since the same form of uncini can develop in the various families, in various ways, they cannot be used to trace the phylogeny of the polychaetes."

Rosenfeldt's transformation series for sabellid uncini only considered two states derived from the ancestral form. The initial apomorphic condition is postulated to be an enlargement of teeth above the main fang. From this state is derived rasp-shaped uncini

via loss of the main fang and multiplication of horizontal rows of teeth. With regard to the old Sabellinae and Fabriciinae, Rosenfeldt considered the above transformation series to have occurred in parallel in both subfamilies. Unfortunately, what states were found in the genera examined was not made clear, nor was any consideration given to modifications with respect to the breast or handle. No distinction was made between thoracic or abdominal uncini.

Disagreement between the transformation series in the present study and that of Rosenfeldt lies primarily in the nature of character state polarization. Rosenfeldt's hypothetical uncinal form does not appear to be justified on any empirical grounds. It is possible that the hooded hooks of the Spionidae or Capitellidae could have been the plesiomorphic form Rosenfeldt was considering in this regard, but this was not stated explicitly. Since the analysis was restricted to essentially only one character, general dentition, the question of a monophyletic origin for just these seven families examined is rather dubious. Viewing the traditional Fabriciinae and Sabellinae as valid (and I assume monophyletic) severely limited the informative nature of such a study. Further, Rosenfeldt's transformation series is falsified by inclusion of additional characters; in the present study this has been the case for the Sabellidae.

There is a significant difference between elucidating instances of homoplasy and judging the usefulness of a character in systematic and/or phylogenetic studies. Rosenfeldt was incorrect in concluding that the presumed presence of homoplasy negates use of uncini as characters for establishing a hierarchical pattern of relationship. The fact that homoplasy might be interpreted at one level does not mean that such a state cannot be used as a synapomorphy at another level (Hennig, 1966; Churchill et al., 1985; Farris and Kluge, 1985, 1986).

For example, the presence of thoracic acicular uncini in the Trichobranchidae and some sabellid genera is probably homoplasious when relationships of these two groups are considered with respect to all other families. Such a condition, however, does not prevent the presence of acicular uncini from being a synapomorphy, denoting the more exclusive

monophyletic status of the trichobranchids, nor in establishing relationships of the sabellid genera. The recognition of homoplasy does not necessarily make a case against using the character in question. Instead, reevaluation of character interpretation at that particular level must be investigated more thoroughly.

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APPENDIX I

Species examined and literature consulted in determining character state distributions. Abbreviations indicate where specimens are deposited; catalog numbers are given when known; *s.n.* (sine numero) is used if no number is known. Literature used in obtaining character states for each genus is listed after the species have been given. Abbreviations are explained in the Acknowledgments.

- Amphiglena mediterranea* (Leydig, 1851); USNM 5095. — Claparède (1864), Rioja (1923), Fauvel (1927), Day (1967).
- Anamobaea orstedii* Kröyer, 1856; FSBC I 33810 — Kröyer (1856), Augener (1925), Perkins (1984).
- Augeneriella hummelincki* Banse, 1957; ZMH V-11917a (holotype), ZMH V-11918 (paratypes), USNM *s.n.* — Banse (1957).
- Bispira voluticornis* (Montagu, 1804); FSBC I 32292. *Bispira crassicornis* (Sars, 1850); USNM 23554. *Bispira variegata* (Kröyer, 1856); USNM 59848. — Montagu (1804), Sars (1850), Rioja (1923), Fauvel (1927), Perkins and Knight-Jones (1986).
- Branchiomma nigromaculata* (Baird, 1865); USNM 43507. — Rioja (1923), Fauvel (1927), Jones (1962).
- Caobangia brandti* Jones, 1974a; USNM 50857 (paratypes). — Giard (1893), Jones (1974a).
- Chone infundibuliformis* Kröyer, 1856; USNM 372, USNM 5176, USNM 41517, USNM 4159, USNM 41520. *Chone aurantiaca* (Johansson, 1901); USNM 43637. *Chone duneri* Malmgren, 1867; USNM 23630. — Kröyer (1856), Malmgren (1867), Banse (1972).
- Demonax microphthalmus* (Verrill, 1873); USNM 54724, USNM 65902. *Demonax rugosus* (Moore, 1904); USNM 41465, USNM 44857. — Kinberg (1867), Knight-Jones (1983), Perkins (1984), Knight-Jones and Walker (1985).
- Desdemona ornata* Banse, 1957; ZMH V-12881a (holotype), ZMH V-12881b (paratypes), ZMH P-15213, ZMH P-17595, ZMH P-15537. *Desdemona aniara* Hutchings and Murray, 1984; USNM 81478 (paratypes). — Banse (1957), Day (1967), Hutchings and Murray (1984).
- Dialychone acustica* Claparède, 1870; AG *s.n.* — Claparède (1870), Fauvel (1927).
- Euchone analis* (Kröyer, 1856); USNM 333, USNM 23651, USNM 23660. — Kröyer (1856), Malmgren (1867), Banse (1970, 1972).
- Euchonella magna* Fauchald, 1972; AHF 980 (holotype). — Fauchald (1972).
- Eudistylia vancouveri* (Kinberg, 1867); USNM 44862. — Kinberg (1867), Bush (1905), Hartman (1938, 1942).
- Fabricia sabella* (Ehrenberg, 1836); ZMH V-12879 (topotypes), USNM 40718, USNM 40719, USNM 40720, USNM 57947. — Ehrenberg (1836), Banse (1956).
- Fabriciola baltica* Friedrich, 1939; USNM 43304. *Fabriciola berkeleyi* Banse, 1956; USNM 32836 (paratypes). — Berkeley (1930), Annenkova (1934), Zenkevitch (1934), Friedrich (1939), Banse (1956).
- Fabrisabella vasculosa* Hartman, 1969; AHF 192 (holotype), AHF 193 (paratypes). — Hartman (1969), Fauchald (1972).
- Genus A, USNM *s.n.*
Genus B, USNM *s.n.*
Hypsicomus stichophthalmos (Grube, 1863); ZMB

- 372 (syntypes), ZMB Q 5240 (syntypes). — Grube (1863, 1870), Perkins (1984).
- Jasmineira filiformis* Hartman, 1965; USNM 69634, USNM 69638. *Jasmineira caeca* Ehlers, 1913; USNM 57160. *Jasmineira* cf. *pacifica* Annenkova, 1937; USNM 90385. *Jasmineira regularis* Hartman, 1972; USNM 47102. — Langerhans (1880), Rioja (1923), Fauvel (1927), Hartman (1965, 1972), Uebelacker (1984a).
- Laonome kroyeri* Malmgren, 1867; NRS 6809 (syntypes). *Laonome* cf. *kroyeri*; USNM 43521, USNM 43522. — Malmgren (1867), Fauvel (1927).
- Manayunkia speciosa* Leidy, 1859; USNM 31015. — Leidy (1859, 1883), Pettibone (1953), Banse (1956), Holmquist (1967, 1973).
- Megalomma vesiculosa* Montagu, 1815; USNM 97444. *Megalomma bioculatum* (Ehlers, 1887); USNM 75971, *Megalomma pigmentum* Reish, 1963; USNM 57945. *Megalomma* sp. A, USNM 53976. — Montagu (1815), Rioja (1927), Johansson (1927), Perkins (1984).
- Myxicola infundibulum* (Renier, 1804); USNM 15612, USNM 44807, USNM 44808. — Renier (1804), Rioja (1923), Fauvel (1927).
- Notaulax nudicollis* (Kröyer, 1856); USNM 62084. *Notaulax occidentalis* (Baird, 1865); USNM 16216, USNM 16245. — Tauber (1879), Perkins (1984).
- Oriopsis armandi* (Claparède, 1864); MNHP 264, 3 additional lots (*s.n.*) also examined. *Oriopsis hynensis* Knight-Jones, 1983, PKJ (paratypes). *Oriopsis limbata* (Ehlers, 1897), USNM 57166. *Oriopsis* sp., USNM 46368. — Claparède (1864), Caullery and Mesnil (1896), Rioja (1923), Fauvel (1927), Banse (1957), Knight-Jones (1983).
- Panousea africana* Rullier and Amoureux, 1970; MNHP *s.n.* (holotype). — Rullier and Amoureux (1970).
- Perkinsiana fonticula* (Hoagland, 1919); USNM 66404, USNM 66405, USNM 66407. *Perkinsiana littoralis* (Hartman, 1967); USNM 55570 (holotype), USNM 55571 (paratype). *Perkinsiana minuta* (Treadwell, 1941); USNM 42793, USNM 44906. — Knight-Jones (1983).
- Potamethus elongatus* (Treadwell, 1906); USNM 5221 (holotype). *Potamethus mucronatus* (Moore, 1923); USNM 17351 (holotype), USNM 17466. *Potamethus scotia* (Pixell, 1913); USNM 47107, USNM 57454. *Potamethus* sp. A Uebelacker, 1984a; USNM 90430. — Ehlers (1887), Chamberlin (1919), Knight-Jones (1983), Perkins (1984).
- Potamilla neglecta* (Sars, 1851); USNM 5179, USNM 16205. — Sars (1851), Bush (1905), Rioja (1923), Knight-Jones (1983).
- Potaspina pacifica* Hartman, 1969; AHF 204 (holotype). — Hartman (1969).
- Pseudobranchiomma emersoni* Jones, 1962; AMNH 3613 (paratypes). — Jones (1962).
- Pseudopotamilla oculifera* (Leidy, 1855); USNM 5186. — Bush (1905), Hartman (1938), Knight-Jones (1983).
- Sabella pavonina* Savigny, 1822; USNM 19618, USNM 49669. — Savigny (1822), McIntosh (1922, 1923), Rioja (1923), Fauvel (1927), Perkins and Knight-Jones (1986).
- Sabellastarte indica* Savigny, 1822; USNM 26077, USNM 29717. *Sabellastarte magnifica* (Shaw, 1800); USNM 4644, USNM 44784, USNM 50105. — Savigny (1822), Day (1967), Fauchald (1977).
- Sabellonga disjuncta* Hartman, 1969; AHF 195 (holotype). — Hartman (1969).
- Schizobranchia insignis* Bush, 1905; USNM 40333, USNM 40336, USNM 44781. — Bush (1905), Hartman (1942).

APPENDIX II

Characters and associated states used in the present study. Characters are grouped according to body region. Numbers and letters, designating characters and states, respectively, are the same as used in the text.

Characters of the branchial crown:

1. Branchial lobes: a. separate; b. fused dorsally.
2. Radiolar and pinnular surface: a. smooth; b. with minute wrinkles.
3. Shape of radioles in cross section: a. square; b. round; c. flat.
4. Skeletal axis of radiole: a. absent; b. 4 or more cells in cross section; c. 2 cells in cross section; d. a single row of cells.
5. Branchial hearts: a. absent; b. present.
6. Palmate membrane: a. absent; b. present.
7. Radiolar flanges: a. absent; b. present.
8. Stylodes: a. absent; b. present, poorly developed; c. present, well developed.
9. Radiolar eyes: a. absent; b. simple eyespots; c. unpaired compound eyes proximally; d. unpaired compound eyes only on distal regions; e. paired compound eyes on all regions.
10. Dorsal lips: a. present, without radiolar appendages; b. present, with radiolar appendages; c. absent.
11. Dorsal pinnular appendages: a. absent; b. present.
12. Ventral lips: a. present; b. absent.

13. Parallel lamellae: a. absent; b. present.
14. Ventral filamentous appendages: a. absent; b. present, nonvascularized; c. present, vascularized, unbranched; d. present, vascularized, branched.
15. Ventral radiolar appendages: a. absent; b. present.
16. Dorsal, marginal branchial base flanges: a. absent; b. present.
17. Branchial crown ventral, basal flanges: a. absent; b. present.

Characters of the thorax and abdomen:

18. Anterior peristomial ring margin: a. low, even segment; b. modified as membranous "collar"; c. ventral margin extended as wide lobe; d. ventral margin extended as narrow lobe.
19. Posterior peristomial ring collar: a. present; b. absent.
20. Glandular girdle on setiger 2: a. absent; b. present.
21. Thoracic and abdominal interramal eyespots: a. absent; b. present.
22. Setiger 1 fascicle: a. as bundle similar to other thoracic fascicles; b. as elongate row.
23. Inferior thoracic notosetal fascicles: a. transverse row(s); b. longitudinal bundles; c. irregular bundles.
24. Abdominal neuropodial tori: a. transverse ridge; b. conical lobe; c. low, circular elevation.
25. Abdominal neurosetal fascicles: a. transverse row(s); b. partially spiraled; c. completely spiraled; d. irregular bundle.
26. Pygidial eyes: a. absent; b. present.

Thoracic notosetal characters:

27. Superior thoracic notosetae: a. elongate, narrowly hooded; b. spinelike; c. broadly hooded.
28. Setiger 2 inferior notosetae, anterior row: a. elongate, narrowly hooded; b. bayonet; c. absent.
29. Setiger 2 inferior notosetae, posterior row: a. absent; b. broadly hooded; c. paleate; d. spine-like.
30. Setiger 4 inferior notosetae, anterior row: a. elongate, narrowly hooded; b. broadly hooded; c. pseudospatulate; d. bayonet; e. absent.

31. Setiger 4 inferior notosetae, posterior row: a. absent; b. broadly hooded; c. paleate; d. spine-like.

Abdominal neurosetal characters:

32. Anterior abdominal setae, anterior row: a. absent; b. elongate narrowly hooded; c. paleate; d. spinelike; e. elongate broadly hooded.
33. Anterior abdominal setae, posterior row: a. elongate needlelike; b. modified elongate narrowly hooded; c. elongate narrowly hooded; d. spinelike; e. elongate broadly hooded; f. absent.
34. Posterior abdominal setae, anterior row: a. absent; b. modified elongate narrowly hooded; c. elongate narrowly hooded; d. paleate; e. spinelike; f. elongate broadly hooded.
35. Posterior abdominal setae, posterior row: a. elongate needlelike; b. modified elongate narrowly hooded; c. elongate broadly hooded; d. absent.

Thoracic neurosetal characters:

36. Teeth of thoracic uncini: a. equal size, no main fang; b. equal size in broad series surmounting main fang; c. unequal size in broad series surmounting main fang.
37. Breast of thoracic uncini: a. small, as slight swelling proximal to main fang; b. well-developed, expanded.
38. Handle of thoracic uncini: a. absent; b. very elongate; c. medium length; d. short.
39. Hood on thoracic uncini: a. absent; b. present.
40. Companion setae: a. absent; b. distal end dentate; c. distal end as roughly symmetrical membrane; d. distal end as distinctly asymmetrical membrane.

Abdominal notosetal characters:

41. Teeth of abdominal uncini: a. rasp-shaped without distinct main fang; b. with main fang surmounted by broad series of smaller teeth.
42. Breast of abdominal uncini: a. small, poorly developed; b. well-developed, expanded; c. reduced to narrow swelling; d. enlarged as proximal manubrium.
43. Handle of abdominal uncini: a. absent; b. long; c. short.

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